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A PHYLOGENETIC INVESTIGATION OF *BEGONIA* L. SECTION *KNESEBECKIA* (KLOTZSCH) A.DC.

A thesis submitted to the University of Glasgow for the degree of Doctor of Philosophy

Zoe Badcock

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DECLARATION

I hereby declare that this thesis is composed of work carried out by myself unless otherwise cited and the thesis is of my own composition. The research was carried out in the period October 1994 to December 1997. This dissertation has not in whole or in part been previously presented for any other degree.

ABSTRACT

This thesis uses morphological and molecular data to address the phylogeny of *Begonia* and in particular section *Knesebeckia*. *Begonia* is a species rich genus containing an estimated 1400 species distributed throughout the tropics and subtropics although none are present in Australia and New Zealand. Despite its horticultural importance few studies of the genus have been made and there is no published phylogeny for *Begonia*.

Begonia section *Knesebeckia* is the only section from the c. 80 sections in *Begonia* to be currently recognised as containing species from more than one continent. There are 77 species (33 American and 44 Asian) currently attributed to *Knesebeckia*. With the prospect of an interesting biogeographic study, the aim of this research was to test the monophyly of *Knesebeckia*.

A cladistic analysis of the morphology of *Begonia* was conducted using a sample of 86 taxa representing the morphological and geographical variation in *Begonia*. This analysis included all the available American *Knesebeckia* and 11 Asian *Knesebeckia*. A total of 66 macro- and micro-morphological characters was included in the analysis and resulted in 5340 trees contained in two islands of equally most parsimonious trees. From these results several conclusions were able to be made: 1) *Knesebeckia* is not monophyletic; 2) *B. dichroa* and *B. olbia* are not closely affiliated to other American *Knesebeckia* and are contained in a clade which is sister to a clade containing species with fleshy indehiscent fruit, mainly from Africa; 3) groupings of species suggested for the remainder of the American *Knesebeckia* include some species which may better be represented in section *Begonia*; a clade centred around *B. incarnata*, the type of *Knesebeckia*; and a clade centred around *B. boissieri* for which the section *Quadriperigonia* should be reinstated; 4) several species were suggested as being closely related to section *Gireoudia*, e.g. *B. peltata*, and representatives from sections with a chromosome number of 2n = 28 (e.g. *Gireoudia* and *Weilbachia*) are recommended for inclusion in any future study of American *Knesebeckia*; 5) Asian

Knesebeckia are shown to be paraphyletic, with representatives from sections *Alicida*, *Diploclinium*, *Lauchea*, *Monophyllon*, *Parvibegonia*, *Putzeysia* and *Trilobaria* nested in the clade of Asian *Knesebeckia*; 6) section *Diploclinium* is shown to be polyphyletic; species groups centred around *B. putii* and *B. rubella* are recommended for consideration in the context of any future analysis of Asian *Knesebeckia*.

A cladistic analysis of sequence data for 30 species of *Begonia* from the noncoding chloroplast DNA region *trn*C - *trn*D was compared to an analysis of the morphology for the same 30 species. The results were not congruent and it was argued that the molecular phylogeny is more reliable than the morphology phylogeny for these 30 species and that combining the data sets for a "total evidence" view is not conducive to the production of a reliable and conservative estimate of the phylogeny of *Begonia*.

The molecular phylogeny corroborates the conclusion in the larger morphological study that *Knesebeckia* is not monophyletic. The implications of the molecular phylogeny for the phylogeny of *Begonia* are discussed.

The properties and evolution of this region of noncoding chloroplast DNA are investigated and compared to previous studies of other noncoding regions. The region is found to be AT rich with many insertions and deletions (indels). These indels are shown to be phylogenetically informative, exhibiting little homoplasy.

A review of the literature relating to *Knesebeckia* indicate that *B. grandis*, an Asian species included in *Knesebeckia* from its inception, is the type of section *Diploclinium*. Eleven Asian species are provided with updated descriptions and admitted to section *Diploclinium*. Some existing species are placed as synonyms of these species and one new combination is made.

ACKNOWLEDGEMENTS

This work was funded by the M.L. MacIntyre *Begonia* Trust fund. I am very happy that the generosity of the late Mr. MacIntyre opened the world of *Begonia* systematics to me.

There are many people I would like to thank for their help during my research. Firstly I am grateful to my supervisors Prof. Jim Dickson, Dr. Jayne Armstrong and latterly Dr. Rod Page. When I first began this research the advice I received from Zoë Cooke (née Gowler) and Mark Tebbitt was particularly useful and I would like to thank Pete Hollingsworth for encouraging me to start my molecular work.

The staff at the Royal Botanic Garden, Edinburgh have been welcoming, informative and extremely helpful. The RBGE library staff have been very obliging with their help. I am grateful to the following people: Crinan Alexander for advice on field work in China and discussions on cultivated plant taxonomy (*B. grandis* paper); David Cann for information on plants in cultivation but not known in the wild (*B. grandis* paper); David Chamberlain for help with Chinese localities; Ian Hedge for advice on visiting the Paris herbarium; Roger Hyam for molecular chats; Sabina Knees for discussions on cultivated plant taxonomy (*B. grandis* paper); Douglas McKean for information on H. Léveille's specimens and collectors; Robert Mill for help with nomenclature, species descriptions, collecting localities and, not least, drawing to my attention the publication of c. 30 new species of *Begonia* from China; Richard Pankhurst for advice on coding inflorescence characters; Toby Pennington for advice on collecting, tropical fieldwork, cladistics and academia and for collecting *Begonia* in silica gel etc.; Mark Watson for advice on the *Flora of China* and Chinese fieldwork; Peter Wilkie for collecting *Begonia* in silica gel.

The fieldwork in Mexico was successful largely thanks to the efforts of Tére Mejia Saules. I am very grateful to Tére and her family for proving such generous hosts. I would also like to thank Mario Sousa Sanchez in UNAM, Mexico City and Sergio Avendano R. at the Institute of Ecology, Veracruz for invitations to visit their

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My research has been greatly facilitated by the National *Begonia* Collection held in Glasgow Botanic Garden which is maintained at a very high standard. I would like to thank all the staff at the garden, especially John Stevensen, David Menzies, Paul Mathews and Euan Donaldson. I am also grateful to the Royal Botanic Garden, Edinburgh, the Royal Botanic Gardens, Kew, Wageningen Agricultural University and Huckriede-van der Laan (Wateringen, The Netherlands) for providing me with living and silica dried material.

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determining the precise details on the sheets of *B. sinensis* and *B. josephi* in G-DC, Selina Marner (OXF) for help in determining if a Kaempfer *Begonia* specimen was present in the Oxford herbaria, Walter Till (WU) for his advice on the typification of *B. asperifolia* and Nick Turland (BM) for his advice on the Linnean herbarium.

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PREFACE

Since 1994 the flowering plant genus *Begonia* L. has been the subject of research at Glasgow University. This has largely been invigorated by the M. L. MacIntyre *Begonia* Trust Fund. The first student of *Begonia* systematics was (Dr.) Mark T. Tebbitt who successfully defended his thesis, "*A Systematic Investigation of* Begonia *section* Sphenanthera *(Hassk.) Benth. & Hook.f.*", in 1997. Mark was funded by the BBSRC. Following my own studentship, the first to be funded by the trust fund, Laura L. Forrest is now investigating various aspects of *Begonia* phylogenetics in Glasgow and Edinburgh.

In the outset it was my aim to investigate the phylogenetic relationships of *Begonia* section *Knesebeckia* (Klotzsch) A.DC., concentrating upon the Mexican and Central American species in the section. While this has largely remained the focus of my research, the emphasis has changed to include the Asian species. As this change in emphasis occurred in my second year, I had already completed a field trip to Mexico and was well acquainted with the Mexican species in the section. This has allowed me to include all the available American *Knesebeckia* in the final analysis of the morphology of *Begonia*. A complete revision of the Asian species was not feasible in the time available, partly due to the publication of over 30 new *Knesebeckia* (as section *Begonia*) from China, the type material of which was unavailable due to the *Flora of China* project.

I have aimed to write much of this thesis in the format of scientific papers. A product of this is an overlap in the possible content (largely the introductions) of each chapter. I have therefore included a full introduction to evolutionary ideas in chapter two and to taxonomic ideas in chapter four; otherwise I have referred the reader back to either chapters two or four. The thesis comprises five chapters. Chapter one briefly introduces *Begonia* and presents the aims of the thesis; chapter two reviews the morphological aspects; chapter three recounts the molecular part; and chapter four comprises the

taxonomic and nomenclatural aspects of my research. The final chapter draws the thesis to a conclusion and presents some ideas for future work which can build upon my research. Paragraph 4.5.5 will shortly be submitted to the *Edinburgh Journal of Botany* with the title "A reassessment of the taxonomy of *Begonia grandis* Dryand. (Begoniaceae) and the infraspecific ranks of E. Irmscher".

Under the rules of the *International Code of Botanical Nomenclature* (hereafter cited as ICBN), Articles 32 and 33 (Greuter *et al.*, 1994), new combinations presented in this thesis are not validly published. Herbarium abbreviations follow *Index Herbariorum* (Holmgren *et al.*, 1981); abbreviations of taxonomic authors follow *Authors of Plant Names* (Brummit & Powell, 1992); book abbreviations follow *Taxonomic Literature II* (Stafleu & Cowan, 1976-88; Stafleu & Mannega, 1992-); and journal abbreviations follow *Botanico-Periodicum-Huntianum* (Lawrence *et al.*, 1968; Bridson, 1991).

CHAPTER 1 INTRODUCTION

1.1 INTRODUCTION

The family Begoniaceae Agard. consists of three genera, *Hillebrandia* Oliv., *Symbegonia* Warb. and *Begonia* L. Based on morphological data it is most closely related to the genus *Datisca* which contains two species: *D. cannabina* L. from SW Asia and the Himalayas and *D. glommerata* (Presl) Baill. from California, U.S.A. (Lindley, 1846; Lawrence, 1951; Dahlgren, 1980; Takhtajan, 1980; Cronquist, 1981; Thorne, 1992; Bouman & de Lange, 1983; Boeswinkel, 1984). Although published studies of *rbc*L (Chase *et al.*, 1993; Swensen *et al.*, 1994; Swensen, 1996) and 18S rDNA (Soltis *et al.*, 1997) sequence variation do not resolve this relationship clearly, more thorough unpublished studies of *rbc*L sequence data support the relationship (S. Swensen, pers. comm.).

Hillebrandia is a monotypic genus from the Hawaiian archepelago, *Symbegonia* contains 12 species from New Guinea and *Begonia* contains an estimated 900 (Heywood, 1993; de Wilde, 1985) to 1400 (Sosef, 1994) species distributed throughout the tropics and subtropics, though absent from Australia and New Zealand. The species in *Begonia* are divided into c. 80 sections of which all except one, section *Knesebeckia* (Klotzsch) A.DC., are limited to one continent. Warburg (1894) and then Irmscher (1925) grouped the sections by the continent upon which they occur but no comment was made as to whether this reflected their ideas of evolutionary relationships in the genus. *Knesebeckia* has thus been something of an enigma in *Begonia*, containing species from Mexico, Central and South America and mainland South East Asia.

1.2 AIMS

- to produce revised descriptions for a selection of Asian species currently included in section *Knesebeckia*.

- to test the monophyly of *Begonia* section *Knesebeckia* when containing species from Asia and America.
- to determine which species and groups of species should be included in any future studies to delimit the Asian and American *Knesebeckia*.
- to determine American *Knesebeckia* species relationships based upon morphological data.
- to produce a preliminary estimate of the phylogeny of *Begonia* based on both morphological and molecular data and to test the congruence of these phylogenies with a view to combining the data sets for a "total evidence" phylogeny of *Begonia*.
- to investigate the characteristics and evolution of noncoding chloroplast (cp) DNA.

CHAPTER 2 ASSESSING THE MONOPHYLY OF *BEGONIA* SECTION *KNESEBECKIA* USING MORPHOLOGICAL DATA

2.1 INTRODUCTION

Begonia L. is a large genus of flowering plants distributed throughout the tropics and subtropics, though absent from Australia and New Zealand. Estimates of the number of species in the genus range from 900 (Heywood, 1993; de Wilde, 1985) to 1400 (Sosef, 1994) with several hundred species probably remaining to be described, especially from the Malesiana region (pers. ob.; Doorenbos, pers. comm.; Sands, pers. comm.; Tebbitt, pers. comm.).

Klotzsch (1854; 1855) was the first person to study the genus as a whole and divided the species known to him into 41 genera, including the 4 genera (*Begonia*, *Eupetalum* Lindl., *Mezieria* Gaudich., and *Diploclinium* Lindl.) already recognised. This classification remained until Alphonse de Candolle (1859; 1864) published the revision of Begoniaceae for his *Prodromus*. Although de Candolle (1859) agreed with Klotzsch's groupings, he thought that the overall integrity of *Begonia* morphology warranted a treatment including only 3 genera, *Begonia*, *Casparya* A.DC. and *Mezierea*; de Candolle therefore included the remaining genera as sections of *Begonia*. This classification is largely followed today, although there are now c. 80 sections within *Begonia*, and two other genera, *Hillebrandia* Oliv. and *Symbegonia* Warb., have been described, giving a total of 3 genera in the family Begoniaceae.

Begonia section *Knesebeckia* (Klotzsch) A.DC. was first described by Klotzsch in 1854 and included 13 species from Mexico and Central America and one, *B. discolor* (=*B. grandis* Dryand.) from China. This was peculiar as Klotzsch's description of *Knesebeckia* stated that the genus included shrubs and subshrubs from Mexico and Guatemala. All the other genera described by Klotzsch contained species from only one continent, leaving *Knesebeckia* as somewhat anomalous. De Candolle followed

Klotzsch's example and included species from Asia and America in *Knesebeckia*. Bentham and Hooker (1867) were next to treat the genus and arranged the sections of de Candolle in an artificial system of series, not drawing any conclusions as to possible relationships between the sections (both the American and Asian members of *Knesebeckia* were included within one series). Warburg (1894) was the next person to study the genus in its entirety and was the first to suggest that the Asian and American members of *Knesebeckia* should not be included within the same section. Warburg placed the Asian species into sect. *Diploclinium* subsect. *Knesebeckiopsis* and the American species into sect. *Begoniastrum* subsect. *Euknesebeckia*. Through this change, Warburg had constrained all the sections to a continent; he then arranged the sections by continent, i.e. Africa, Asia and America. Following Warburg, Irmscher (1925), in the second edition of *Die Natürlichen Pflanzenfamilien*, also arranged the sections by continent but reversed Warburg's changes to *Knesebeckia*, placing all the Asian and American species into *Begoniastrum* subsection *Knesebeckia*. Irmscher appears to have used this rank consistently (e.g. 1927, 1929, 1931, 1937, 1939) until 1960 when he refers to section *Knesebeckia*. The rank of section was retained by Barkley and Baranov (1972) and then Baranov and Barkley (1974) in their lists of *Begonia* sections and species.

Throughout this introduction I have recorded the taxonomic history of *Knesebeckia* in terms used by previous authors. Klotzsch (1854) however made a nomenclatural error when he attributed the valid publication of *Diploclinium* to R. Wight and not Lindley. This has been repeated by subsequent authors. In fact Lindley validly published *Diploclinium* in 1846 and, as he mentioned only one species, *Diploclinium evansianum* (=*B. grandis*), this should be the type species (Art. 10.3, ISBN) of this genus (now section). As mentioned earlier, *B. discolor* (=*B. grandis*) was the only Asian species included in *Knesebeckia* by Klotzsch and thus, if both American and Asian species were to be included in the same section, that section would be called *Diploclinium*, having priority over the name *Knesebeckia*.

Since Klotzsch established section *Knesebeckia*, only Warburg (1894) has refuted the grouping together of Asian and American species in this one section. This would suggest that there are some strong morphological characters to support this grouping. Irmscher (1925) stated that there were no differences in the flowers or habit which could justify a division into sections and that, on the contrary, the American and Asian *Knesebeckia* were much more closely related than many other forms which were left in one section, even by Warburg. Irmscher continued to say that, in spite of the wide geographical separation, a very close relationship existed between the species in *Knesebeckia*.

The combination of characters that Irmscher (1925) used to describe his subsection *Knesebeckia* were:

> four male tepals, filaments free, sometimes fused into a distinct column, anthers oblong, obtuse, as long as or longer than the filaments, connective scarcely projecting, 5-6 female tepals, 3 bifid styles, shortly fused below, style-branches often twisted, the stigma forming a continuous helical band, placentas bifid with ovules on all sides, fruit 3 locular with 3 uneven wings, mostly erect herbs or sub-shrubs, mostly slanting and pointed leaves, cystoliths absent, sometimes with tubers at the base of the stem and axillary bulbils.

In retrospect, the characters which appear to have been critical in the delimiting of this group are the tuberous habit and axillary bulbils.

In spite of this long list of characters, the publication of many new species since 1925 has blurred the section boundaries of this group. Smith & Schubert (e.g. 1946) eventually declined to distinguish between Irmscher's subsections of *Begoniastrum* (=*Begonia*) in their floristic treatments of the Begoniaceae in Central and South America. Although these boundaries are not well defined, the question remains, should these species from Asia and America be placed in one section?

Few people have proposed any evolutionary relationships about *Begonia* and only two studies have been published using the explicit framework of a cladistic analysis: Sosef (1994) and Klazenga *et al.* (1994). Several authors have suggested that the section *Mezierea* represents the most primitive extant members of the genus, certainly within Africa (e.g. Arends, 1985; de Wilde, 1985; de Wilde & Arends, 1989; Reitsma, 1984; 1985; Van den Berg, 1985; Klazenga *et al.*, 1994) and forms a distict group together with sections *Baccabegonia*, *Squamibegonia* and *Tetraphila* (Arends, 1985; de Wilde, 1985; Van den Berg, 1985; Reitsma, 1984; 1985; de Lange & Bouman, 1985; 1992). This hypothesis is based upon the shared characteristics of exalate, fleshy fruit, placentation which is either parietal or septal, increased seed size and reduction in seed ornamentation, pollen grains which are small, nearly spherical, without a margo and with a small elliptical endoaperture without costae, and a base chromosome number of x = 12/13 in *Mezierea* and x = 18 in the remaining sections. De Wilde & Arends (1989) agree with Van den Berg (1984) that the centre of origin of *Begonia* is the area formerly made up out of Madagascar, the Comores and the Seychelles, adding Mauritius and Réunion upon their investigation of *B. salaziensis* (sect. *Mezierea*).

De Lange & Bouman (1992), however, do not agree with the postulate that *Mezierea* is the most primitive among all the sections in the genus. Pointing to the fact that the seed characters associated with zoochory are a unique feature in *Begonia*, they propose that anemochory (wind dispersal) is not only the most common but also the most "original" type of dispersal in *Begonia* and that this is congruent with the situation in the Datiscaceae, the closest relative of the Begoniaceae (Bouman & de Lange, 1983; Boeswinkel, 1984). Together with this refutation of *Mezierea*'s primitive status, de Lange and Bouman (1992) also disagree with any ability to propose a centre of origin for the Begoniaceae, believing that with so little known about the origin of the family it is quite conjectural to do so.

With respect to *Knesebeckia* and this study, Irmscher (1929; 1939) and Jin & Wang (1994) propose hypotheses for the section's evolution and possible phylogenetic

relationships. Despite the fact that Irmscher (1925) had earlier pronounced the similarity of the Asian and American *Knesebeckia*, he never mentioned the matter again.

Within Asian *Knesebeckia*, Irmscher (1929; 1939) proposed:

- sect. *Monophyllon* had arisen from sect. *Parvibegonia*, which had, in turn, arisen from sect. *Begoniastrum* (=*Knesebeckia*) (Irmscher, 1929).
- a close relationship between *B. grandis* subsp. *holostyla* and *B. yunnanensis* (=*B. modestiflora*) and between *B. labordei* and *B. fimbristipula* (Irmscher, 1939).
- the occurence of undivided placentae in part of the ovaries of *B. labordei*, *B. wilsonii* and *B. fimbristipula* was possibly the result of an ancient hybridisation event between species with bifid placentae and species with entire placenta (Irmscher, 1939).
- the distribution of *Begoniastrum* (=*Knesebeckia*) was almost exclusively restricted to China with only a few species having a more southerly distribution, the section being replaced by sect. *Petermannia* in tropical Asia (1939). [This could mean that Irmscher thought *Knesebeckia* and *Petermannia* are sister taxa, occurring in similar habitats in sympatric areas.]
- The flower characters of *Knesebeckia* are, among Asian *Begonia*, some of the least derived characters and *Knesebeckia* can be seen as the departure point for some other specialised habitat and flower forms (Irmscher, 1939).
- the species in *Knesebeckia* show a trend to stem reduction (acaulescence) which is a polyphyletic tendency in *Begonia* (Irmscher, 1939).

Jin & Wang (1994) proposed that, among Chinese *Begonia*, one evolutionary line goes from section *Sphenanthera* to sect. *Begonia* then reaches sect. *Platycentrum* and sect. *Reichenheimia* respectively, while the other line goes from sect. *Coelocentrum* to sect.

Diploclinium. They admit that the actual relationships are probably more complicated than these 2 lines can show (summarised in fig. 2.1).

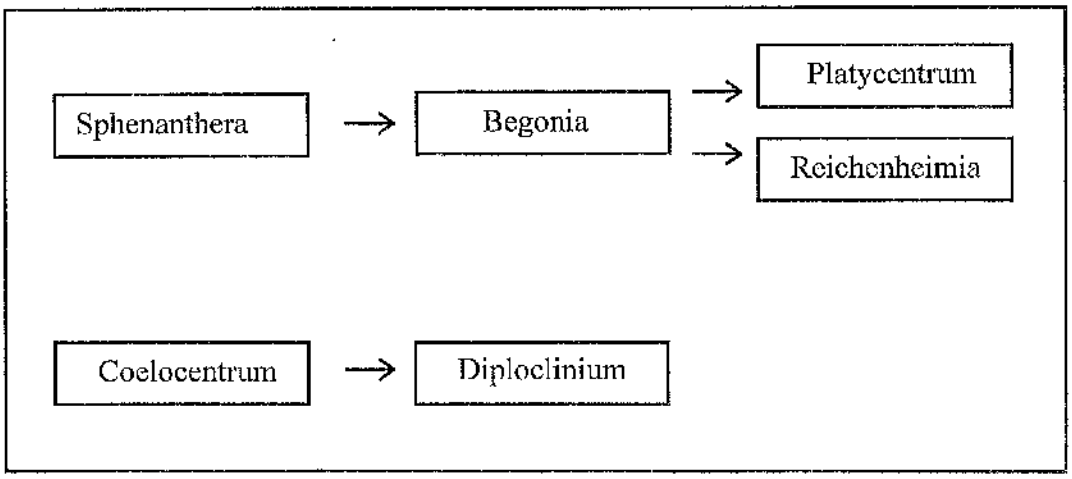


FIG. 2.1 EVOLUTIONARY RELATIONSHIPS PROPOSED BY JIN & WANG (1994).

The aims of the present study were as follows:

- To determine if *Begonia* sect. *Knesebeckia* is monophyletic when containing species from Asia and America.
- If the section is not monophyletic, can a statement be made with respect to which species groups should be included in future studies to delimit the Asian and American species?
- Within the American *Knesebeckia*, can any conclusions be made regarding species relationships?
- Do *Monophyllon*, *Parvibegonia* and *Knesebeckia* form a clade and can anything be said about the former two sections' origins?
- Is *B. grandis* closely related to *B. modestiflora*?
- Is *B. labordei* closely related to *B. fimbristipula*?

- Is there any evidence for a hybrid origin of *B. labordei*, *B. fimbristipula* or *B. wilsonii*?
- Are *Knesebeckia* and *Petermannia* sister taxa representing sympatric groups with similar ecological niches?
- Is *Knesebeckia* basal within Asia, possessing primitive floral and habit characters?
- Does *Knesebeckia* show a trend towards acaulescence and is there evidence that acaulescence is polyphyletic within *Begonia*?
- Is there any evidence to support the evolutionary relationships proposed by Jin & Wang (1994)?
- Is *Mezierea* basal within *Begonia* and does it form a clade with sections *Baccabegonia* (not sampled here), *Squamibegonia* and *Tetraphila*?
- Can anything be concluded about a centre of origin for *Begonia*?

2.2 MATERIALS AND METHODS

2.2.1 CHOICE OF TAXA AND OUTGROUP SELECTION

With no published phylogenetic framework in *Begonia*, it was necessary to sample the geographic and morphological variation present in the genus in order to test the monophyly of section *Knesebeckia*. As there are over 1000 species divided into c. 80 sections in *Begonia*, a pragmatic approach to sampling was taken. Taxa were included on the basis of unpublished molecular studies (Brouillet, pers. comm. and Swensen, pers. comm. both suggested that South American species should be included), published hypotheses relating to taxa in *Knesebeckia* (A. de Candolle, 1864; Irmscher, 1939; Burt-Utley, 1985; Jin & Wang, 1994), and my personal observations of herbarium material in BM, E, K, L, MEXU, P and XAL. *Datisca* was included as the outgroup (the outgroup method is reviewed by Nixon & Carpenter, 1993), based on analyses of *rbc*L sequence data (Chase *et al.*, 1993; Swensen *et al.*, 1994; Swensen, 1997; Swensen pers. comm.,

1997; Badcock, unpublished analysis of sequence data in Genbank), 18S rDNA sequence data (Soltis *et al.*, 1997) and intuative opinions on morphology (Lindley, 1846; Lawrence, 1951; Dahlgren, 1980; Takhtajan, 1980; Cronquist, 1981; Thorne, 1992; Bouman & de Lange, 1983; Boeswinkel, 1984).

All (available) American *Knesebeckia* and 11 species of Asian *Knesebeckia*, both *sensu* Barkley & Golding (1974), were included in this study. The subset of Asian species represented the morphological and geographical variation of section *Knesebeckia sensu* Irmscher in Asia. It was not possible to include all Asian *Knesebeckia* because many of the species were not available for loan from China and not represented in Western herbaria.

All the 86 taxa included in the morphological analysis are listed in table 2.1 with their distribution and current section placement. The specimens examined for these taxa are listed in Appendix A except Asian *Knesebeckia* which are listed in chapter 4.

TAXON	SECTION OF *BEGONIA*[1]	DISTRIBUTION[2]
acerifolia H.B.K	*Knesebeckia*	Ecuador
acutifolia Jacq.	*Begonia*	West Indies
adenopoda Lem.	*Lauchea*	Burma
alicida C.B.Clarke	*Alicida*	Burma & Bangladesh
angustiloba A.DC.	*Knesebeckia*	Mexico
annulata K.Koch	*Platycentrum*	Eastern Himalaya
adscendens C.B.Clarke	*Knesebeckia*	Burma & India
asperifolia Irmsch.	*Knesebeckia*	S. W. China
balmisiana Balmis	*Knesebeckia*	Mexico
biserrata Lindl.	*Knesebeckia*	Mexico & Central America
boissieri A.DC.	*Knesebeckia*	Mexico
brevirimosa Irmsch.	*Petermannia*	New Guinea
bulbillifera Link & Otto	*Knesebeckia*	Mexico
convolvulacea (Klotzsch) A.DC.	*Enita*[3]	Brazil
cordifolia (Wight) Thwaites	*Diploclinium*	India & Sri Lanka
crenata Dryand.	*Parvibegonia*	S. India
cuernavacensis Ziesenh.	*Knesebeckia*	Mexico
dealbata Liebm.	*Knesebeckia*	Mexico
dichroa Sprague	*Knesebeckia*	Brazil
dipetala Graham	*Haagea*	S. India & Sri Lanka
dregei Otto & Dietrich	*Augustia*	S. Africa
falciloba Liebm.	*Knesebeckia*	Mexico
fernaldiana L.B.Sm. & B.G.Schub.	*Knesebeckia*	Mexico
fimbristipula Hance	*Knesebeckia*	S. W. China
floccifera Bedd.	*Reichenheimia*	S. India & Sri Lanka
gemmipara Hook.f. & Thomson	*Putzeysia*	E. Himalaya
goegoensis N.E.Br.	*Reichenheimia*	Sumatra
gracilis H.B.K.	*Knesebeckia*	Mexico
grandis Dryand. subsp. *grandis*	*Knesebeckia*	China
grandis subsp. *holostyla* Irmsch.	*Knesebeckia*	S. W. China
heracleifolia Schltdl. & Cham.	*Gireoudia*	Mexico
hintoniana L.B.Sm. & B.G.Schub.	*Knesebeckia*	Mexico
ignea Warz. ex A.DC.	*Knesebeckia*	Mexico & Central America
imperialis Lem.	*Weilbachia*	Mexico & Central America
incarnata Link & Otto	*Knesebeckia*	Mexico
johnstonii Oliver ex Hook.f.	*Rostrobegonia*	E. Africa: Tanzania
josephi A.DC.	*Knesebeckia*	Eastern Himalaya
labordei H.Lév.	*Knesebeckia*	S. W. China, E. Burma & N. Vietnam
lobata Schott	*Ewaldia*	Brazil

TABLE 2.1 SUMMARY OF TAXA INCLUDED IN MORPHOLOGICAL CLADISTIC ANALYSIS WITH DISTRIBUTION AND SECTION DETAILS

ludwigii Irmsch.	*Knesebeckia*	Ecuador
malachosticta Sands	*Petermannia*	Malaysia: Sabah
mannii Hook.f.	*Tetraphila*	W. Africa: Nigeria, Equatorial Guinea, Cameroon
martabanica A.DC.	*Parvibegonia*	India, Burma
masoniana Irmsch.	*Coelocentrum*	? S. W. China, Indochina
maynensis A.DC.	*Knesebeckia*	Peru, Ecuador
meyeri-johannis Engl.	*Mezierea*	E. Africa: Zaire, Rwanda, Burundi, Uganda, Kenya, Tanzania
michoacana L.B.Sm. & B.G.Schub.	*Knesebeckia*	Mexico
microcarpa A.DC.	*Begonia*	Ecuador
modestiflora Kurz	*Knesebeckia*	N. E. India, Burma, S.W. China, Laos, Thailand
nemoralis L.B.Sm. & B.G.Schub.	*Knesebeckia*	Mexico
novo-granatae A.DC.	*Hydristyles*	Colombia & Venezuela
oaxacana A.DC.	*Hexaptera*	Mexico & Central America
olbia Kerch.	*Knesebeckia*	Brazil
palmata D.Don	*Platycentrum*	Eastern Himalaya
pedata Liebm.	*Knesebeckia*	Mexico
pedunculosa Wall.	*Knesebeckia*	N. E. India
peltata Otto & Dietrich	*Knesebeckia*	Mexico & Central America
picta Sm.	*Knesebeckia*	Himalaya
poculifera Hook.f.	*Squamibegonia*	Central Africa: Nigeria - Angola
portillana S.Watson	*Begonia*	Mexico
prismatocarpa Hook.	*Loasibegonia*	W. Africa: Equatorial Guinea, Cameroon, Ivory Coast
prolifera A.DC.	*Monophyllon*	Burma
putii Craib	*Diploclinium*	Thailand
quadrialata Warb.	*Loasibegonia*	W. Africa: Sierra Leone - Angola
rajah Ridl.	*Reichenheimia*	Malaya
rhodochlamys L.B.Sm. & B.G.Schub.	*Begonia*	Mexico
roxburghii A.DC.	*Sphenanthera*	N. E. India - Burma
rubella Buch.-Ham. ex D.Don	*Trilobaria*	Nepal
salaziensis (Gaud.) Warb.	*Mezierea*	Réunion & Mauritius
sandtii Ziesenh.	*Knesebeckia*	Mexico
satrapis C.B.Clarke	*Knesebeckia*	N. E. India
sericoneura Liebm.	*Gireoudia*	Mexico & Central America
socotrana Hook.f.	*Peltaugustia*	Socotra
sutherlandii Hook.f.	*Rostrobegonia*	S. Africa & Tanzania

TABLE 2.1 CONTD.

tayabensis Merr.	*Diploclinium*	Philippines
tenera Dryand.	*Reichenheimia*	Sri Lanka
ulmifolia Willd.	*Donaldia*	Venezuela
uniflora S.Watson	*Knesebeckia*	Mexico
uruapensis Sessé & Moç.	*Knesebeckia*	Mexico
wallichiana Lehm.	*Doratometra*	Mexico
weberlingii Irmsch.	*Knesebeckia*	El Salvador
wilsonii Gagnep.	*Knesebeckia*	S. W. China
wollnyi Herzog	*Knesebeckia*	Brazil & Bolivia
Datisca cannabina L.	Genus	S. W. Asia - Himalayas
Hillebrandia sandwicensis Oliv.	Genus	Hawaiian archepelago
Symbegonia sanguinea Warb.	Genus	New Guinea

[1]According to Barkley & Golding (1974), with the exception of "Asian *Knesebeckia*" which were sometimes attributed to section *Begonia* (see chapter 4, paragraph 4.2 for a discussion of this nomenclature).

[2]Distributions according to Barkley & Golding (1974) except where additional information available in chapter 6, specimens cited in Appendix A, Burt-Utley (1985), Klazenga *et al.* (1994), Sosef (1994) and de Wilde & Arends (1980).

[3]This may be an error as the species appears very similar to species in section *Pritzelia* and a herbarium sheet in K has a remark by Barkley that the species belong to section *Pritzelia*.

[4] Placed in new (but unpublished) section *Dioecibegonia* M.T.Tebbitt (1997).

TABLE 2.1 CONTD.

2.2.2 THE CHARACTERS

A total of 70 binary and multistate characters was scored; four of these characters were excluded in all but the most preliminary searches. The scored characters are discussed below in paragraphs 2.2.2.1 - 2.2.2.6 and are summarised in table 2.2. Those characters not included, and others which may prove useful with further investigation, are presented in paragraph 2.2.2.7. All the characters were treated as unordered and with equal weight.

Pimentel & Riggins (1987) argue that data which require statistical description (i.e. means, standard deviations or ranges) to estimate gaps in the data, do not possess "cladistic properties", and call the use of such statistics "data massaging" to the point of inventing data. The most emphatic reason given by Pimentel and Riggins (1987) for

rejecting all quantitative data, even if mutually exclusive states exist, is the inability to apply tests of homology, as defined by Patterson (1982); any homologies would then be implied and could not be an "abstract line".

Although the use of entirely discrete characters may be philosophically desirable for cladistic analyses and advocated by some (e.g. Pimentel & Riggins (1987), Cranston & Humphries (1988), Pennington (1996)), much of the variation observed in nature is continuous and several authors have argued, with varying conviction, for the phylogenetic utility of characters which vary continuously (e.g. Chappill (1989), Stevens (1991), Thiele (1993)). Stevens (1991) pointed out that the distiction between qualitative and quantitative data may be more semantic than real and in his final conclusions called for far greater justification and documentation of character states [than at present].

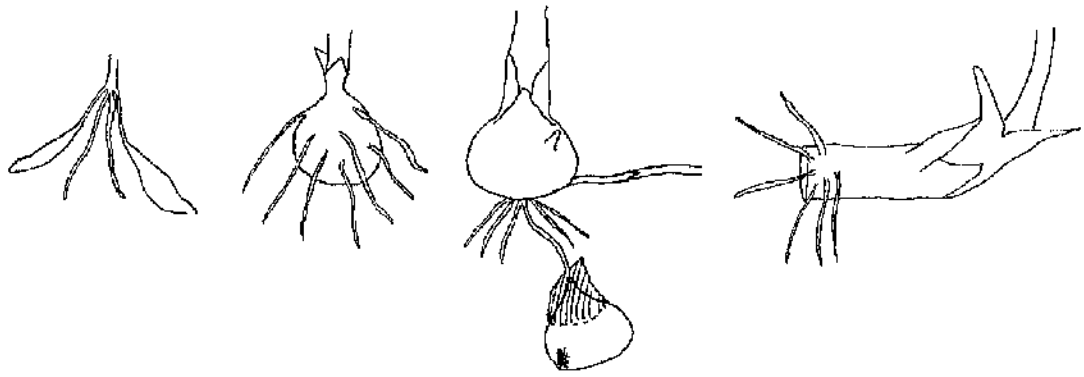
Preferring this pragmatic approach to character delimitation, I have taken care to document and illustrate the characters used here. The majority of the characters were selected for their discrete nature and thus their ability to be scored unequivocally. Although no characters have been defined by statistical analysis, characters 4, 23 and 25 should, given time, be so defined. Other characters may prove more intractable to statistical analysis, e.g. characters 36, 38, 51 and 52. I intuitively believe two of the four characters excluded, anther shape and fruit capsule body shape, to be phylogenetically informative, but these will require morphometric investigation in order to be used cladistically.

As demonstrated by Thiele (1993) and Stevens (1991), many characters are only semantically discrete and my character list contains many examples of these. When this situation is thought to arise, attention has been drawn to the fact in paragraphs 2.2.2.1 - 2.2.2.6. Taxa with polymorphic characters, for which no satisfactory computation method has been developed, have usually been treated as missing but when evidence is present (in monographs) that one state is much more prevalent (> 75%) than another, the more common state is scored; this situation is also indicated in paragraphs 2.2.2.1 -

2.2.2.6. Finally, evidence was found which supported the establishment of an intermediate character state to accommodate infraspecific polymorphism in character 51.

2.2.2.1 VEGETATIVE CHARACTERS

1. Root type (see fig. 2.2). Fibrous roots, no obvious storage organ (0); swollen storage roots (1); root tuber (2); stem tuber (corm) (may form moliniform rhizome) (3); rhizome (4). Historically many *Begonia* species have been designated as tuberous and little attention has been paid to the origin of the tuber but this situation has led to non-homologous organs being classified together. A similar situation has arisen in other plant groups, e.g. tuberous *Lomatiums* (Apiaceae) (Soltis & Novak, 1997). With the identification of this homology problem, the Asian members of *Knesebeckia* (possessing stem tubers and swollen storage roots) have been able to be separated from the American members (posessing root tubers) of the section. Conformation of this character should be sought from anatomical studies of the vascularisation of these organs. A rhizomatous habit appears in several sections of *Begonia* and careful analysis of this character state may well provide similar examples of false homologies.

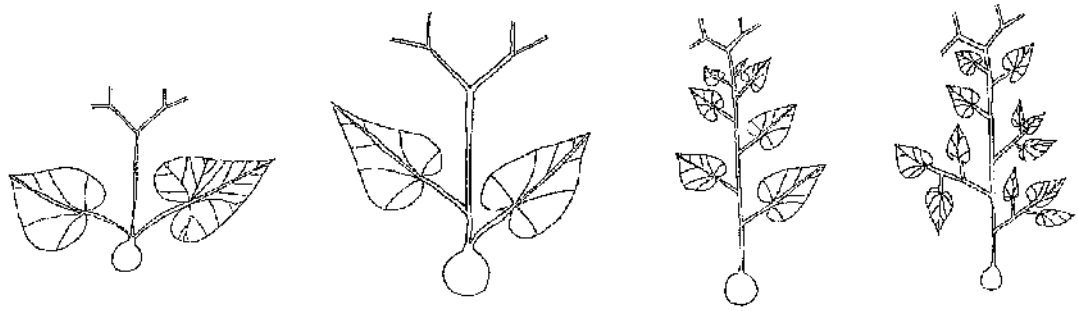


swollen storage roots (1) root tuber (2) stem tuber (3) rhizome (4)

FIG. 2.2 ROOT TYPE

2. Stem presence (see fig. 2.3). Acaulescent or shortly caulescent (0); stem not branching (1); stem branching (2). Although this character is partly dependent upon the root type, it was deemed sufficiently independent for scoring as some rhizomatous species may also be caulescent, with single or multiple stems. In some species e.g. *B. asperifolia*, *B. picta*, *B. josephi*, which have been described as acaulescent, there is a

tendency to be caulescent reflecting a degree of environmental plasticity; in these cases the taxa were scored as acaulescent.



acaulescent (0) shortly acaulescent (0) caulescent (1) stem branching (2)

FIG. 2.3 PRESENCE OF STEM

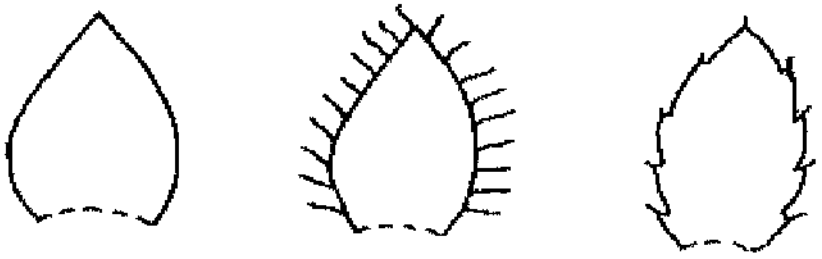
3. Stipule persistence. Stipules caducous (0); deciduous (1); persistent (2); absent (3). Caducous stipules are usually absent from a herbarium sheet or, if present, will only be found at the very youngest nodes. Deciduous stipules may persist for a short time but do not retain their rigidity. Persistent stipules may eventually fall off a stem but the majority of the nodes will retain the stipules which retain their rigidity. Stipules are absent in *Datisca*, or may possible be represented by two tiny hairs (Forrest & Badcock, 1997, pers. obs.).

4. Stipule shape (see fig. 2.4). Stipules ovate-lanceolate / triangular-lanceolate / linear-lanceolate (0); oblong-ellipsoid (1); triangular-ovate (2); broadly ovate (3). Most species of *Begonia* have stipules which vary around a lanceolate shape but these will appear quite different according to their size, persistence, fleshiness and colour in the living state. Some species within the American *Knesebeckia* possess broadly ovate stipules which appear to be derived from smaller, triangular ovate stipules.

ovate oblong-cllipsoid triangular-ovate Broadly ovate

FIG. 2.4 STIPULE SHAPE

5. Stipule margin (see fig. 2.5). Stipules entire (0) fimbriate (1); dentate or dentate-fimbriate (2). Species with fimbriate margins have been distinguished from those with dentate-fimbriate margins as some species have been observed to have their stipule margins fringed with hairs but with no toothing, while those species with toothed margins often also have hairs at the ends of the teeth.



entire (0) fimbriate (1) dentate-fimbriate (2)

FIG. 2.5 STIPULE MARGIN

6. Stipule nerve excurrent (see fig. 2.6). Stipule nerve excurrent (0); not excurrent (1). This character must be distinguished from a tooth at the end of the stipule which may appear to extend the nerve.

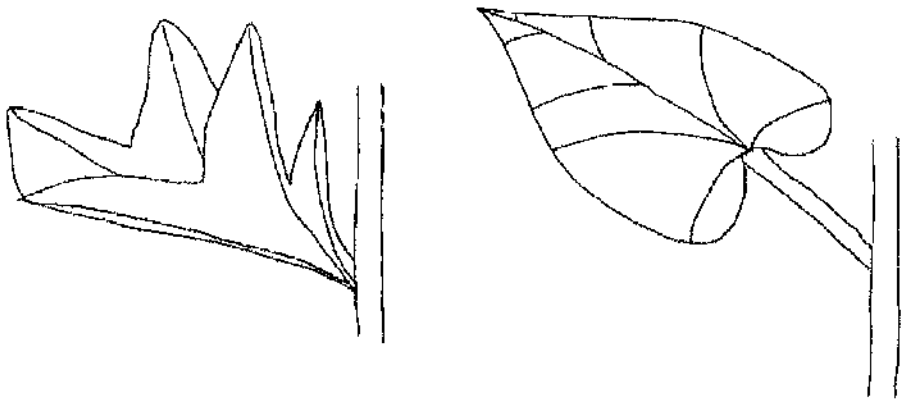
Nerve excurrent (0) not excurrent (1)

FIG. 2.6 STIPULE NERVE EXCURRENT

7. Bulbils. Bulbils present (0); absent (1). There appear to be several different forms of bulbils but it was decided to code simply for their presence or absence, assuming homology. Where axillary buds give rise to runners without any obvious persistent bulbils, these were scored as present for bulbils, e.g. *B. crenata* and others from the group of sections closely associated with section *Parvibegonia*. The bulbils of *B. socotrana* and *B. gemmipara* are distinctive. *B. socotrana* produces bulbils at its base and this is indicative of its posession of a stem tuber rather than a root tuber as the bulbils are produced from stem axil nodes (Irmscher (1925, p. 6 of translation) describes *B. socotrana* as having a thickened rhizome). *B. gemmipara* produces small groups of bulbils in bundles of four, enclosed by prophylls, in the axil of a stipule (Irmscher, 1925). These bundles of bulbils may also be produced from an inflorescence stem and vice versa (pers. obs.). Irmscher (1925) distinguishes the bulbils of *B. gemmipara* from those of *B. socotrana* as they are "bulb-like, composed of many thick scaly forms which are enclosed by a membranous sheath". Further developmental and anatomical studies are required before these vegetative reproductive characters can be confirmed as homologous. *B. grandis* has been observed to produce fairly large axillary bulbils in the field (Tebbitt, pers. comm.), and *B. uruapensis* has distinctively large axillary bulbils (pers. ob.). Again these cannot be confirmed as homologous without further investigations.

8. Petiole presence (see fig. 2.7). Leaf cauline (0); petiolate (1). Species with cauline leaves, e.g. *B. angustiloba* and *B. balmisiana*, sometimes possess petiolate leaves but

the majority of leaves will be cauline. Klazenga *et al.* (1994) and Sosef (1994) used petiole length as a character in their studies of sections *Mezieria* and *Scutobegonia* / *Loasibegonia* respectively; Klazenga *et al.* (1994) delimited states as greater or less than 15 cm; Sosef (1994) had states of ≤ 7.5, ≤ 15, ≤ 22.5 and > 22.5 cm. While the utility of this character can certainly be appreciated, it was felt that in the current study petiole length could not be utilised in a cladistic analysis encompassing the entire genus.



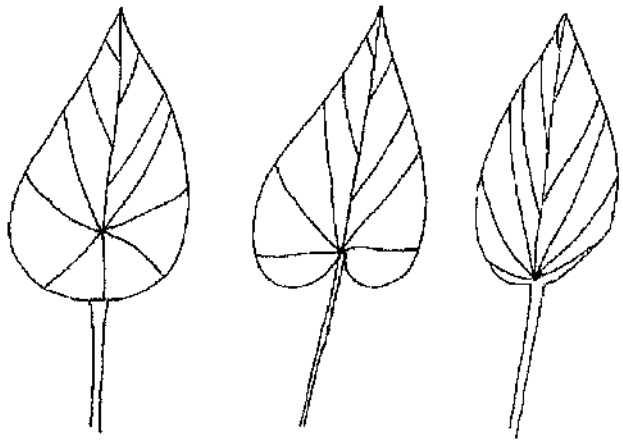
leaf cauline (0) leaf petiolate (1)

FIG. 2.7 PRESENCE OF PETIOLE

9. Leaf texture. Leaf leathery, no (0); yes (1). The leaves of sections *Sphenanthera sensu* Irmscher (1925) (*Dioecibegonia* M.T.Tebbitt, 1997) and *Mezieria* (except *B. meyeri-johannis*) are leathery. Originally an attempt was made to break down the character of the leaf texture into more states than simply "leathery" but I was unable to provide any reliable characters without further investigation of the anatomy of the leaves. Sosef (1994) utilised such anatomical characters of the leaf petiole to help delimit sections *Loasibegonia* and *Scutobegonia*.

10. Leaf venation. Leaf venation pinnate (0); palmate-pinnate (1).

11. Leaf base shape (see fig. 2.8). Leaf peltate (0); cordate with basal lobes (1); cordate without basal lobes (2). While there is a wide variety in the depth of the basal lobes of leaves, it appears to be characteristic for some sections. Burt-Utley (1985, p. 17) reports that Smith observed both peltate and cordate leaves on a single specimen.



peltate (0) basal lobes (1) no basal lobes (2)

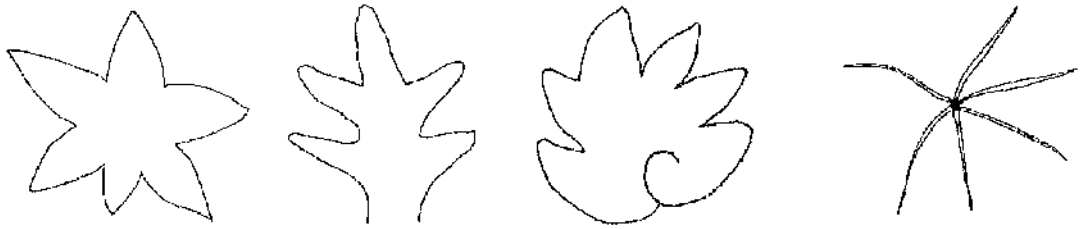
FIG. 2.8 LEAF BASE SHAPE

12. Ring of hairs or trichomes at the junction of the leaf blade with the petiole. Present (0); absent (1). Initially this character was scored in order to distinguish hairs from trichomes but as more species were observed with this character, it seemed unwise to distinguish these states as a continuum appeared to exist, though admittedly the extremes are readily separable, e.g. *B. falciloba* has a distinctive ring of hairs while *B. ludwigii* and *B. manicata* have fused trichomes, possibly forming a barrier to insects ascending the petiole (Forrest, 1997, pers. comm.). In Africa, only South and East African species possess this character, e.g. *B. sutherlandii* and *B. johnstonii*, while in America species in sections *Gireoudia* and *Knesebeckia* possess the character. No species from Asia were observed with a ring of hairs or trichomes at their petiole apices.

13. Stellate trichomes (see fig. 2.9). Present (0); absent (1). The African fleshy fruited species with parietal placentation often possess stellate and peltate-helicoid trichomes on their fruit capsules (and elsewhere). It is assumed here that the pelate-helicoid trichomes (de Wilde & Arends, 1980) observed in section *Squamibegonia*, e.g. *B. poculifera*, are either a derivative or a precusor of conventional stellate trichomes and are therefore scored together as one state, although in narrower phylogenetic studies it may be useful to score these as a separate state. Stellate trichomes are rare elsewhere, occurring in section *Baccabegonia*, in *B. stellata* and *B. prismatocarpa*, both in section

Loasibegonia and, within the Asian species studied, *B. picta* but only on the fruit capsule. Sosef (1994, p. 14-15) noted the rarity of "dentate scales" and said they "might present a clue to unravel the phylogeny of the African sections in *Begonia*".

14. Stellate hairs (see fig. 2.9). Present (0); absent (1). It was determined here that the stellate hairs occasionally observed in some South American species were not homologous with stellate trichomes. These hairs were seen on the tepals of *B. imperialis* (section *Weilbachia*) and the stems of *B. franconis* (section *Doratometra*) and have a much finer, more regular appearance than the stellate trichomes.



stellate trichome branching trichome pelate-helicoid trichome stellate hair

FIG. 2.9 STELLATE HAIRS AND TRICHOMES

2.2.2.2 INFLORESCENCE CHARACTERS

15. Form of sex separation. Monoecious with bisexual inflorescences (0); monoecious with unisexual inflorescences (1); dioecious or androdioecious (2). The issue of sex separation in *Begonia* and *Datisca* is complex. In *Datisca*, the evolution and genetics of sex separation has been investigated by Rieseberg, Liston and Wolf (Liston *et. al.*, 1989; Rieseberg *et al.*, 1992; Wolf *et al.*, 1997). The Californian *D. glomerata* is androdioecious while the Asian *D. cannabina* is dioecious. Traditionally androdioecy is thought to be an intermediate step in the evolution of dioecy from monoecy, but Rieseberg *et al.* (1992) proposed that androdioecy is the derived condition in *Datisca*. In *Begonia* the dioecious condition is rare and appears confined to one or two sections. Within Asia, dioecy has been confirmed by Tebbitt (1997) who circumscribed a new section, *Dioecibegonia* M.T.Tebbitt (not yet published), partly characterised by a

dioecious habit. Other Asian species have often mistakenly been described as dioecious, e.g. *B. dioica* (Badcock, unpublished data) and this appears to be a common mistake within descriptions of *Begonia*, due the often marked temporal separation of the male and female flowers. Sosef (1994), in his monograph of sections *Loasibegonia* and *Scutobegonia*, described one species, *B. schaeferi* Engler, as androdioecious. Klazenga *et al.* (1994), in their monograph of section *Mezieria*, comment that *B. meyeri-johannis* has usually been described as dioecious but when particular attention was paid to this trait in the field one plant was observed with developing fruits and male flowers at anthesis. De Wilde & Arends' (1980) revised description of section *Squamibegonia* stated that both male and female flowers are present within the inflorescences and their development is proterandrous-androgynous. Although the monographing of the African section *Tetraphila* is not yet complete (de Wilde, 1997, pers. comm.), a provisional circumscription of the section (de Wilde & Arends, 1979) described the inflorescences as usually unisexual; some species have been revised and *B. cavallyensis* A.Chev. (Hagman & de Wilde, 1983), *B. fusicarpa* Irmsch. (Hagman & de Wilde, 1983), *B. elaegnifolia* Hook.f. (Arends, 1992), *B. karperi* J.C. Arends (Arends, 1992), *B. longipetiolata* Gilg. (Arends, 1992), *B. loranthoides* (de Wilde & Arends, 1979), *B. rwandensis* J.C. Arends (Arends, 1992), and *B. squamulosa* Hook.f. (Arends, 1992) are all described as monoecious, with unisexual, occasionally androgynous, inflorescences, while *B. pelargoniiflora* J.J. de Wilde & J.C. Arends (Arends, 1992) occasionally has bisexual inflorescences. Section *Petermannia*, represented here by *B. malachosticta* and *B. brevirimosa*, possess unisexual inflorescences which are differentiated with respect to the number of flowers and the compression of the pedicels in the female inflorescence. The transition between dioecy and monoecy appears to be prevalent within a clade, indicated by *rbcL* data (see Swensen *et al.*, 1994; Swensen, 1996), containing the families Cucurbitaceae, Coriariaceae, Datiscaceae, Corynocarpaceae and Begoniaceae (Gornall, 1997, pers. comm.).

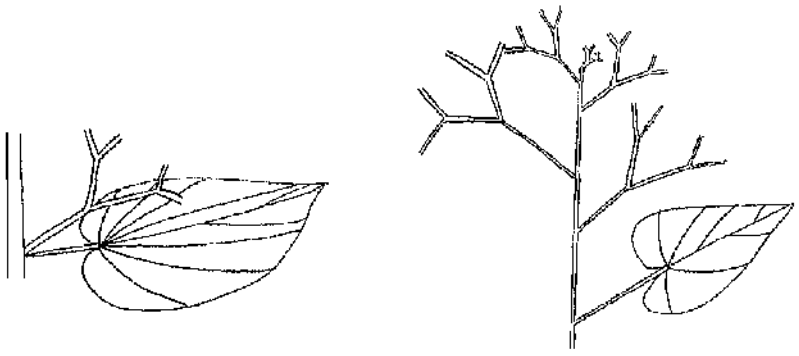
The patterns of inflorescence structure found in *Begonia* have been reviewed and summarised by Irmscher (1914; 1925). Goulet *et al.* (1994) more recently analysed the

inflorescence architecture of Begoniaceae, paying particular attention to the degree of asymmetry. Irmscher divided the inflorescence types into two distinct classes: 1. compound, rarely single racemose inflorescences; 2. cymose inflorescences. Within these classes, further divisions were based upon the relative positions of the male and female flowers. Upon the investigation of 71 species, Goulet *et al.* (1994) recognised 9 architectural models. The groups were based upon a statistical analysis of characters such as the total length of the inflorescence axes, flower numbers on the best and least developed sides of an inflorescence and divergence angles within the inflorescence which allowed them to compare the degree of asymmetry of the inflorescences. The nine groups defined do not appear to reflect any phylogenetic signal, for example, species from section *Gireoudia*, recently monographed by Burt-Utley (1985), do not appear in the same group. This is perhaps most revealing as, within this section, Burt-Utley (see fig. 4, p. 20, 1985) records a trend towards increasing asymmetry of the inflorescences.

There are two main inflorescence types in Mexican *Knesebeckia*. *B. gracilis* and related species possess indeterminate thyrses, while *B. incarnata* and related species have inflorescence units made up of dichotomous cymes located in the axillary nodes of their branching stems. When considered as complete inflorescences, these would be classified as two distinct types, but when comparing individual units of the inflorescences (*sensu* Pankhurst, 1984; Weberling's partial inflorescences, 1989), they are essentially the same, axillary dichotomous cymes. The *B. incarnata* group has a branching stem with partial inflorescences that are usually branched up to 3 times, while the *B. gracilis* group has an upright stem which does not branch, the partial inflorescences are often single flowers, or rarely up to three times branched, and the peduncle may be absent or greatly shortened. A further inflorescence type in American *Knesbeckia* is one more akin to species from section *Gireoudia*. These species, e.g. *B. peltata*, *B. ludwigii*, *B. mucronistipula*, *B. wollnyi*, possess ascending rhizomes (sometimes more obvious in the dried state) with elongated peduncles arising from the terminal area of the stem.

The inflorescences of Asian species in *Knesebeckia* are more intractable. This is partly due to variation in life form (habit - see character 2), but also because many of their inflorescences appear racemose, e.g. *B. grandis*, *B. josephi*, *B. labordei* and *B. modestiflora*, while others have clearly dichotomous cymes, e.g. *B. adscendens*, *B. fimbristipula*, *B. picta* and *B. satrapis*. If one were to think in terms, as many have done, e.g. Irmscher (1914; 1925), that cymes and racemes are two diametrically opposed inflorescence types, then this could cause some confusion, but as Troll (1964, p.33) and Weberling (1989, p. 222) indicate, "there certainly exists a cymose form of branching in the zone of the inflorescence, but there is no such thing as a cymose inflorescence". With this insight, analysing the structure of *Begonia* inflorescences for coding characters can be taken beyond the idea of raceme versus cyme and this will hopefully allow an understanding of how transitions between different inflorescence types can occur and prevent the inextricably linked characters associated with habit (life form) from clouding the issue. Rather than describing the inflorescence types by their classical morphological names, I have broken the inflorescences down into several characters which can evolve independently, to gain an accurate picture of their evolution. Nickol (1995) and Lemson (1997) showed a similar approach to the study of inflorescences in Berberidaceae and Epacridaceae respectively, and the appoach is inspired by Weberling and Troll (see Weberling, 1989, p. 237, fig. 129).

16. Inflorescence position (see fig. 2.10). Inflorescence axillary (0); terminal (1). Inflorescences which are terminal also posess axillary partial inflorescences. Terminal inflorescences include racemes, e.g. *B. modestiflora*, indeterminate thryses, e.g. *B. gracilis*, single flowers, e.g. *B. franconis*, and asymmetrical dichasial cymes, e.g. *B. grandis*.



axillary (0) terminal (1)

FIG. 2.10 INFLORESCENCE POSITION

17. Partial inflorescence branching pattern (see fig. 2.11). Monochasial (0); dichasial (1). Species in section *Loasibegonia* have condensed cincinnal monochasia, while all other species analysed are dichasially branched.

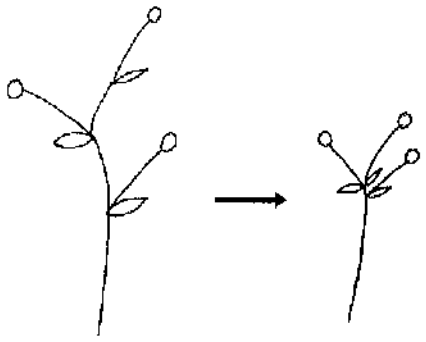


FIG. 2.11 EVOLUTION OF A CINCINNAL MONOCHASIUM? (AFTER SOSEF, 1994)

18. Symmetry of inflorescence branches. Inflorescence branching ± symmetrical (0); asymmetrical (1). Begoniaceae is distiguished by its asymmetrical nature and several publications have attempted to analyse this, e.g. Barabe *et al.*, 1991, 1992a, 1992b; Charlton, 1993; Goulet *et al.*, 1994; McLellan, 1990, 1993; yet within the inflorescence many species have remarkably symmetrical dichasia. No attempt was made to distinguish species with extremely asymmetric inflorescences, e.g. *B. heracleifolia*, from those with only slight asymmetry, e.g. *B. novo-granatae*. Asymmetry was

determined by comparing the lengths of the branches within one dichotomy for several specimens.

19. Number of inflorescence branching points (see fig. 2.12). Single flower - one dichotomy (0); between 2-3 dichotomies (1); > 3 dichotomies (2). The majority of American *Knesebeckia* possess partial inflorescences which are 2-3 branched, but some, e.g. *B. angustiloba*, *B. gracilis*, *B. sandtii*, are single flowered or once dichotomous. The majority of South American species examined here have more than 3 dichotomies, commonly six, as do some Asian species, e.g. *B. floccifera*. The Asian sections allied to section *Parvibegonia* also have many branched inflorescences but only one branch at each dichasium regularly persists (see character 27). This feature is also shared by *B. modestiflora*.

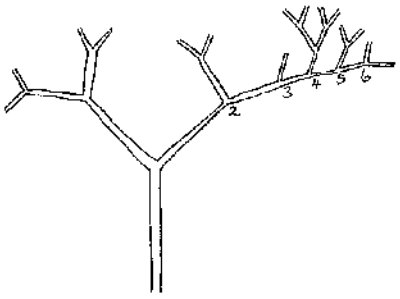
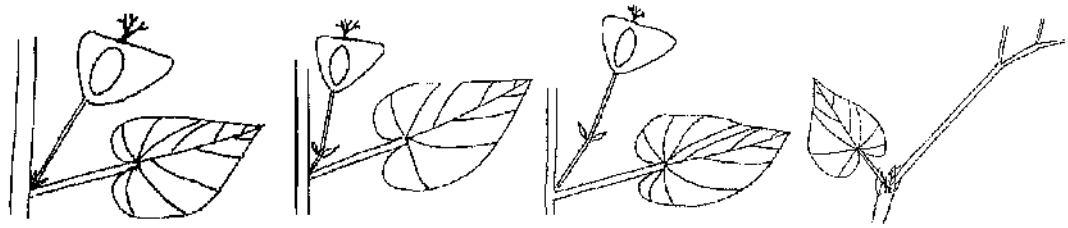


FIG. 2.12 CALCULATION OF NUMBER OF INFLORESCENCE BRANCHING POINTS

20. Peduncle presence (see fig. 2.13). Peduncle absent or less than 1 cm in length (0); present (1); elongated (2). In some species of American *Knesebeckia*, e.g. *B. gracilis*, *B. angustiloba* and *B. balmisiana*, there is a trend towards the absence of a peduncle. The peduncles may appear to be absent but they are merely greatly shortened, as they do elongate when the fruit mature as is common to all *Begonia* infructescences. The peduncles of some species are elongate, extending beyond the length of the petioles, e.g. *B. heracleifolia*, *B. peltata*.



absent (0) almost absent (0) present(1) elongate (2)

FIG. 2.13 PEDUNCLE PRESENCE

21. Bract like stipule presence (see fig. 2.14). Bract like stipules present (0); absent (1). This character distinguishes those species with foliate terminal racemes, e.g. *B. modestiflora, B. martabanica,* from those with asymmetric dichasia, e.g. *B. labordei.*

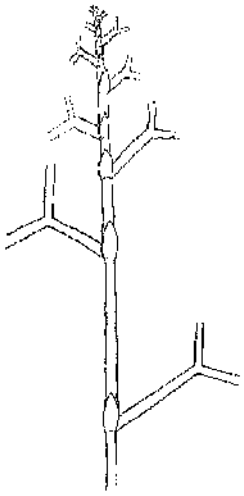


FIG. 2.14 BRACT LIKE STIPULE PRESENCE

22. Bract persistence. Bracts caducous (0); deciduous (1); persistent (2). As with stipules, bracts were determined as caducous if their presence on herbarium material was regularly lacking, decidous if persisting for a short while and persistent only if still present in infructescences.

23. Bract shape at first branching point (see fig. 2.15). Obovate (0); ovate to ovate-lanceolate (1); broadly ovate or obovate (2). Scoring bracts for shape and not combined with size allows species with different sized bracts to be scored as sharing characters they may otherwise not have shared.

oblong-obovate obovate ovate broadly obovate broadly ovate

FIG. 2.15 BRACT SHAPES

24. Bracts at first branching point. Bracts at first branching point forming cup (0); fused (1); patent (2). *B. boissieri* is the only scored species to have fused bracts. Although all bracts originally form a cup around the developing flower buds, this character was scored when the pedicels had elongated and the flowers matured. *B. poculifera* and other species in section *Squamibegonia* are distinguished by particularly large pseudobracts (Irmscher, 1925; de Wilde & Arends, 1980) surrounding the developing male inflorescence, but I was unable to consistently distinguish these from large cup shaped bracts in other species, e.g. *B. incarnata*, *B. grandis*. It is likely that this is an apomorphy of section *Squamibegonia*, possibly shared with some species of section *Bracteibegonia* (Tebbitt, 1997).

25. Bracts at second and later branching points. Oblong-obovate (0); ovate to ovate-lanceolate (1); obovate (2); broadly ovate or obovate (3). The shape of the bracts at the first and later branching points does not appear to be strictly correlated.

26. Bracts at base of ovary. Present (0); absent (1). Burt-Utley (1985) notes that four species in section *Gireoudia* (*B. crassicaulis*, *B. conchifolia*, *B. plebeja* and *B. sericoneura*) are distinguished by the presence of subpersistent bracteoles (termed bracts here) and these form one of her 'species groups', thus applying taxonomic significance to this shared character. Other species in the section may often show signs of rudimentary bracteoles (Burt-Utley, 1985) and the implication is therefore that a trend exists within the section for the loss of these bracteoles. The presence of these bracts is an apparently rare state in the family, but caution is necessary as these bracts may often

be caducous. In this study, care has been taken to look for scars where the bracts may have occurred but these may be easily missed. *Hillebrandia* possesses such bracts. Species, studied here, from sections *Begonia*, *Gireoudia* and *Knesebeckia* from America, *Loasibegonia*, *Scutobegonia* and *Squamibegonia* from Africa, and sections *Putzeysia* and *Petermannia* from Asia, share this character state.

27. Bracts where no obvious dichotomy occurs (see fig. 2.16). Present (0); absent (1). The presence of these bracts is characteristic of species in section *Parvibegonia*, *Alicida* and *Lauchea*, and was also observed in *B. modestiflora* (Asian *Knesebeckia*) and *B. franconis* (sect. *Doratometra*). The underlying cause of this character is not known but may be due to some branches falling off prematurely.

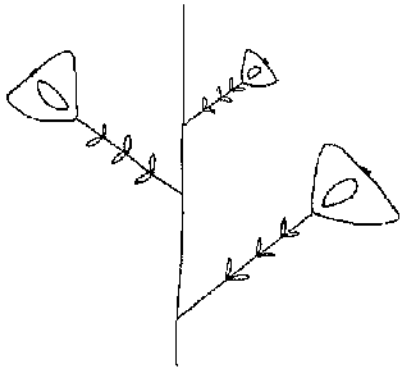
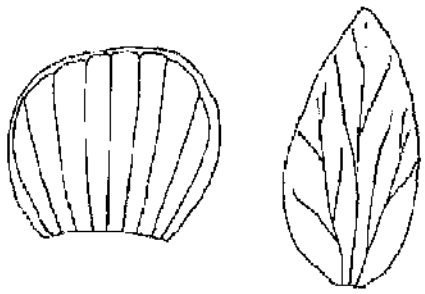


FIG. 2.16 BRACTS WHERE NO OBVIOUS DICHOTOMY OCCURS

28. Flower colour. White or pink (0); yellow or orange (1). Many species exhibit polymorphic flower colour with either white or pink flowers, e.g. *B. grandis* (noted by the occurence of a cultivar 'alba'), *B. josephi*, *B. labordei*, *B. picta*, *B. meyeri-johannis*; this is therefore coded as one state. This polymorphism is common among flowering plants and is thought to be possible because insects, which see ultra-violet light, do not detect a difference between pink and white (Ferris, pers. comm.). Yellow flowers are rare within *Begonia*, but characterise sections *Loasibegonia* and *Scutobegonia*. *B. sutherlandii* is rare in posessing orange flowers. Red flowers are also rare and may be classed as very dark pink, e.g. *Symbegonia*. It is plausible that this flower colour, together with the fused tepals of *Symbegonia*, is an adaptation for bird pollination.

2.2.2.3 MALE FLOWER CHARACTERS

29. Number of sepals (outer whorl) (see fig. 2.17). 2 (0); 4-5 (1). Many authors, e.g. A. de Candolle (1859, 1864) and Irmscher (1925), have noted that the outer and inner whorls of tepals in the male flower correspond to sepals and petals respectively. Despite this, few authors have used this terminology, preferring to refer to tepals (e.g. Irmscher) or perianth segments (e.g. de Wilde & Arends, 1980; Sosef, 1994), while usually describing the outer and inner whorls separately. In the majority of species, I found sepals and petals in the male flower were distinguishable. Following Endress (1994, p. 14) and Weberling (1989, p. 1-92), sepals are characterised by a broad base, several vascular supplies, the veins forming curved arches at the tops of the sepals, and an acute tip (not prevalent in *Begonia* - see character 32). All *Begonia* and *Symbegonia* species have 2 sepals (conservatively, 2 outer tepals), while *Hillebrandia* has 4-5 which alternate with the petals.



sepal petal

FIG. 2.17 DISTINGUISHING SEPALS AND PETALS

30. Number of petals (inner whorl) (see fig. 2..17). 0 (0); 2 (1); 5 (2). This character is homoplasious at this level of analysis but nevertheless is useful. The American sections *Donaldia* (*B. ulmifolia*), *Doratometra* (*B. franconis* has 2 petals), *Gireoudia* (*B. heracleifolia, B. sericoneura*), *Knesebeckia* (*B. peltata*), *Latistigma*, *Meionanthera*, *Philippomartia*, *Pilderia*, *Trachelocarpus*, *Weilbachia* (*B. imperialis*), and the South African *Augustia* (*B. dregei*) and Madagascan *Quadrilobaria* rarely have one or two petals; the American sections *Cyathocnemis*, *Hydristyles* (*B. novo-granatae*),

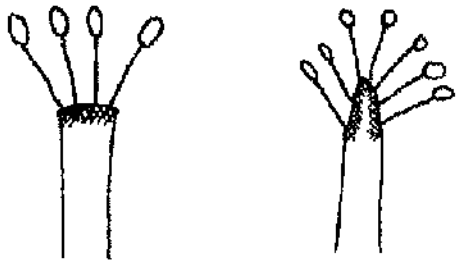
Rossmannia, *Ruizopavonia* and *Warburgia*, the African sections *Filicibegonia*, *Loasibegonia* (*B. prismatocarpa*, *B. quadrialata*) and *Scutobegonia*, and the Asian sections *Apterobegonia*, *Haagea* (*B. dipetala*) and *Monopteron* never have petals; the Asian sections *Diploclinium* (*B. ravenii*) and *Reichenheimia* (*B. floccifera*) rarely have no petals. *Datisca* has no petals and this is likely to be an adaptation to wind pollination. Some species are polymorphic for male petal number, e.g. *B. meyeri-johannis* rarely with 2 petals and *B. salaziensis* rarely with no petals (Klazenga *et al.*, 1994). In these cases, the more common petal number was scored.

31. Sepal outer surface hairy. Hairy (0); glabrous (1). This character was chosen because the presence of hairs on the outer surface of the sepals is quite rare.

32. Sepal apex. Acute to acuminate (0); rounded (1). Within American *Knesebeckia* there is a trend towards acuminate sepals, e.g. *B. falciloba*, *B. fernaldiana*.

33. Sepal margin. Entire (0); dentate (1); fimbriate to dentate-fimbriate (2).

34. Receptacle (see fig. 2.18). Flat or slightly raised (0); rounded or a torus (1). In the absence of detailed anatomical studies, this character is occasionally difficult to distinguish from some states of character 36.



flat or slightly raised (0) rounded or a torus (1)

FIG. 2.18 RECEPTACLE PRESENCE

35. Androphore (see fig. 2.19). Symmetrical (0); asymmetrical (1). Most androphores are symmetrical, but some species posess an aymmetric androphore, possibly as part of a pollination syndrome, e.g. *B. crenata*, *B. prismatocarpa* and *B. quadrialata*.

symmetrical (0) asymmetrical (1)

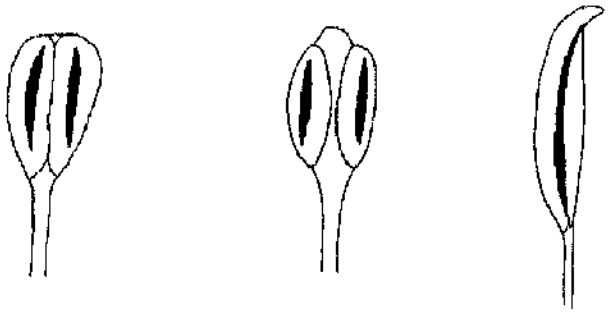
FIG. 2.19 ANDROPHORE SYMMETRY

36. Filament fusion (see fig. 2.20). Filaments free to base (0); fused briefly at base (1); free to base, but some fusion in centre of androphore (2); fused into a column, with filaments arising all the way up the column (3); fused at least half way into a column (4). This character is very plastic, but within a species, can be allocated to one of the given states. Within *Knesebeckia*, as currently delimited, there is a wide variation in this character. *B. maynensis* and *B. hintoniana* have free filaments on a slightly raised torus, *B. boissieri* and *B. ignea* have a column like torus combined with filaments forming a column for at least half their length, *B. incarnata* and *B. nemoralis* have a column at least half their length and *B. portilliana*, *B. weberlingii*, *B. acerifolia*, *B. microcarpa* and *B. uniflora* have filaments free to their base with some fusion in the centre of the androphore.

free (0) fused briefly (0) some fusion in centre (2) filaments arising up column (3) fused at least half of length (4)

FIG. 2.20 STAMEN FUSION

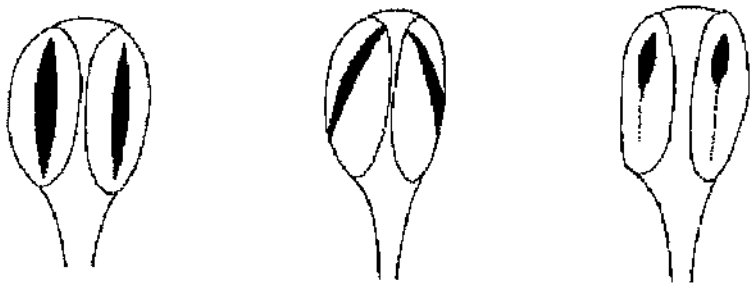
37. Connective extention (see fig. 2.21). Connective not extended (0); extended to a tip (1); extended to a ledge (2). The American *Knesebeckia* do not show any extension of the connective, while some of the Asian species have connectives extended to tips. When the extended connective is viewed in side profile it may form a ledge, e.g. *B. lobata*. There is a great deal of variation in the length of this extension in *Begonia* and comparisons should be made at anthesis when extension is maximal.



not extended (0) extended to a tip (1) extended to a ledge (2)

FIG. 2.21 CONNECTIVE PRESENCE

38. Stamen dehiscence (see fig. 2.22). Stamen dehiscing by long straight slits down the middle of the pollen sac (0); arcuate slits (1); very short arcuate slits in upper part of pollen sac (2). While most species dehisce through long straight slits the length of the pollen sacs, American *Knesebeckia*, some Asian *Knesebeckia*, section *Petermannia* and *Symbegonia* have arcuate slits. Species scored here from section *Parvibegonia* and allied sections, e.g. *B. alicida*, *B. crenata*, *B. martabanica* and *B. cordifolia* and *B. pedunculosa*, are distinguished by their very short arcuate slits at the top of the pollen sacs. Further work on the development of anther dehiscence would aid in the delimitation of these character states.



long straight slits (0) arcuate slits (1) very short slits (2)

FIG. 2.22 STAMEN DEHISCENCE

39. Filament to anther length ratio. Anthers shorter than filaments (0); anthers and filaments about same length (1); anthers longer than filaments (2). American *Knesebeckia* have anthers shorter than the filaments, with the anthers of *B. microcarpa* and *B. maynensis* being particularly small in comparison. The filaments and anthers of Asian *Knesebeckia* are usually about the same length. Within other sections of *Begonia* this ratio is often consistent for the section, e.g. *Tetraphila*, *Scutobegonia* and *Loasibegonia* all have longer anthers; *B. meyeri-johannis* is unusual in section *Mezieria* in having shorter anthers.

2.2.2.4 FEMALE FLOWER CHARACTERS

40. Ovary position. Ovary inferior (0); partially inferior (1). *Datisca* and *Hillebrandia* both have partially inferior ovaries, while the ovaries of *Begonia* and *Symbegonia* are inferior.

41. Ovary septa number / locule number. 1 (0); 2 (1); 3 (2); 4 (3); 5-7 (4). Rather than score the number of locules in an ovary it was decided to score the number of septa, which, although usually correlated with the locule number, do not correspond exactly; for example, *Datisca*, which has entirely parietal placentation and thus one locule, has 3 septa. Some species have a variable locule / septa number, e.g. *B. quadrialata* and *B. prismatocarpa* (Sosef, 1994) and *B. picta* (Badcock, see paragraph 4.5.10), but rather than scoring these as polymorphic characters, the most common state was scored (see

paragraph 2.2.2). All *Knesebeckia* (American and Asian) have three locules, the most common state in *Begonia*.

42. Locule development. At least one locule not developing fully (0); all locules developing fully (1) Jin & Wang (1994) showed that the ovary of "2-locular" species in section *Platycentrum* is actually 3-locular but one locule does not fully develop. Species with this feature were scored as 3-locular for character 41. This is not the case for all sections with 2-locular ovaries.

43. Placentation. Parietal (0); axile (1). Although the states in this character might appear discrete, there is considerable evidence that they are not. When Reitsma (1983) studied the placentation of 53 African species of *Begonia* he classified them into two groups, the first including all species with pseudo-axile (*sensu* Gauthier, 1950; 1959) and parietal placentation, the second containing the "real axile" species. The first type was explained by the occurrence of septa, consisting in the lower part of the ovary of carpellary tissue but towards the axis of the ovary, of placental tissue. The second type was defined as when the septa and placenta-bearing centre of the ovary consists entirely of carpellary tissue and this was explained by the margins of the same carpel being fused, while the sides of each carpel are fused with those of the adjacent carpels up to the centre of the ovary (Reitsma, 1983). Reitsma's groups depended upon the interpretation of carpel fusion but Arends (1992, p. 85-91), who reviewed placentation, questioned the inclusion of *B. dregei* and *B. socotrana* in the real axile group as these species have a unilocular and parietal condition at the very top of their ovaries (see Gauthier, 1950, p.21). Arends, in fact, argues that Reitsma didn't consider the possibility that the multilocular condition in the 'real axile' species could also be caused by inward growth and fusion of parietal placentae. Charpentier *et al.* (1989a; 1989b) studied the ontogeny of the female flower of two *Begonia* species and *Hillebrandia*. The authors suggested that the multilocular condition and axile placentation in the lower part of the ovary is due to the development of tissue initiated by a meristem of the floral apex that has an axial position in the base of the young ovary. Simultaneously there is also tissue development higher up in the young ovary. In the four locular *B. horticolor* (sect. *Tetraphila*) this is initiated by 4 similar meristems which are situated on the wall of the ovary cavity. Each one of these meristems produces a longitudinal ridge which remains free and forms a double placenta on each ridge which bears ovules. These ridges are called parietal septa and axile septa by Charpentier *et al.* (1989b). There is a transition zone (Charpentier *et al.*, 1989a) between the axile and parietal zones in the ovary making them difficult to delimit. This zone cannot be definitely attributed to the floral apex or the ovary wall. In *B. dregei* the development of the ovary is determined by the

elongation of the axile zone, which becomes much more developed than the parietal zone, and the longitudinal ridges on the ovary wall of the parietal zone do not form placentae or ovules. So, depending upon the relative growth rate of the axile and parietal zones, the mature Begoniaceae ovary is either axile over its entire length or in the basal part only. Although this hypothesis seems plausible, Sosef (1994) disagrees with the conclusions of Charpentier *et al.* (1989b) and Arends (1992, p. 86 & p. 89) that the occurrence of a parietal situation in the very apex of the locules of the ovary of *B. dregei* and other species, as given by Gauthier, (1950) and Sosef (1994, p. 64, fig. 7.10F) is evidence that the parietal meristem system is only of limited importance. Sosef (1994, p. 66 fig. 7.11, p. 67) interprets this situation as the inevitable result of the entrance of the stylar channel and consequently concludes that Gauthier's (1950, p. 21) conclusion that apparently 'the margin of each carpel is fused with that of the adjacent carpel more intimately than with the other margin of the same carpel' must be considered false. For this to be the case, the stylar channel would have to pass right through the carpel wall in order to create a different situation and Sosef (1994, p. 67) regards this as unlikely. Further to this, Sosef (1994) does not support the theory that there are two different meristem systems, rather, his conclusions, based on the observations of Charpentier *et al.* (1989b) and his investigation of vascularisation patterns, indicate the existence of only one meristem system.

The argument over ovary development in Begoniaceae is not resolved. With the ability to isolate and clone morphologically significant genes, e.g. *cycloidea* (see Cronk & Möller, 1997 for a review) and the advent of technology for RNA *insitu* hybridisation, it seems that an approach similar to those described by Albert *et al.* (talk presented at the *Advances in Plant Molecular Systematics*, Glasgow University, 1997) would be a way of further investigating the development of the ovary in Begoniaceae.

44. Placentae per locule. 1 (0); 2 free placentae (1). The form the placentae take in the ovary is variable, with some single placentae described as thickened, as in sections *Loasibegonia* and *Scutobegonia* (see Sosef, 1994, p. 46), *Augustia* (*B. dregei*) and

Peltaugustia (*B. socotrana*), and some bifid placentae slightly thickened and pressed together as in section *Gaerdtia*. Sosef (1994) conducted a detailed anatomical study of the ovaries for his study group, measuring quantitative characters such as ovary wall thickness, and tackled the delimitation of states, following Chappill's (1989) advice. This approach was beyond the scope of my investigations, hence the delimitation of only two discrete states. Some species are found to have both single and bifid placentae within one locule, especially in Asian *Knesebeckia* and this has been observed in this study and previously by Irmscher (1927; 1939) in *B. labordei*, *B. fimbristipula* and *B. wilsonii* and by Jin & Wang (1994) in *B. grandis* subsp. *grandis* and subsp. *sinensis* ovaries. To avoid such problems, all comparisons were made between the central portions of ovaries.

45. Placental length. Placentae almost as long as the locule (0); less than half the length of the locule (1). It was noted during the course of this study that, rarely, the placentae of some species were particularly short, e.g. *B. maynensis*, *B. olbia*, *B. hymenophylloides* (section *ignota*, unpublished data). The significance and anatomical basis of this character have not been investigated.

46. Tepal fusion. Female tepals free (0); fused (1). The genus *Symbegonia* is characterised by its sympetaly (see character 28).

47. Tepal number. Female tepals 2 (0); 3 (1); 4 (2); 5 (3); 6 (4); 10 (5). The number of tepals in the female flower appears much more variable than in the male flower. Although often consistent within a section, Asian *Knesbeckia* have between 3 and 6 tepals and some species, e.g. *B. satrapis* (5 or 6), *B. fimbristipula* (3 or 5), *B. labordei* (4 or 3) and *B. grandis* subsp. *grandis* (3 or 5), have variable tepal number. As in character 30, these polymorphic taxa were coded according to the most common state, except *B. grandis* subsp. *grandis* which did not have a 75% majority for either tepal number and was thus scored as missing data. Unlike the male flower, authors have consistently refrained from distinguishing sepals from petals and have referred to them as lobes, tepals or perianth segments. In some taxa a distinction is possible, for example in

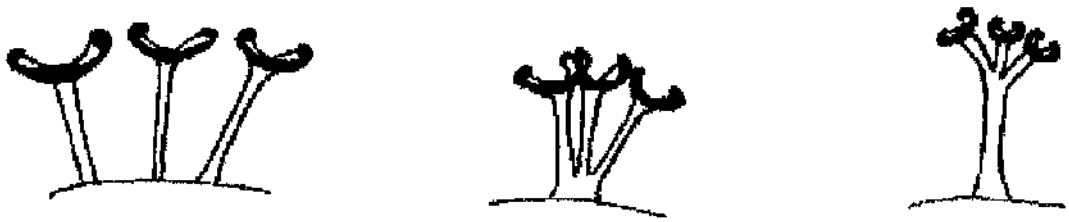
section *Gireoudia* (Burt-Utley, 1985), sections *Loasibegonia* and *Scutobegonia*, and some species in the American *Knesebeckia*, e.g. *B. peltata* which, like section *Gireoudia* has 2 sepals and 1 petal (in some of the other American species in section *Knesebeckia*, the sepals and petals can also be distinguished [3 sepals and 2 petals] but this character cannot be consistently scored).

48. Tepal apex. Female tepal apex acute - acuminate (0); rounded (1). See comments for character 32.

49. Tepal margin. Female tepal margin entire (0) dentate (1); fimbriate or dentate-fimbriate (2). See comments for character 33.

50. Style number. 2 (0); 3 (1); 4 (2); 5 (3). This character is commonly correlated with locule number in the ovary; however this is not always the case, as in some species in sections *Platycentrum* and *Sphenanthera*. Style number may be variable within a species and then the most common state was scored.

51. Style fusion (see fig. 2.23). Styles free (0); fused at base (1); fused for more than half their length (2). Although the degree of style fusion is often variable within a species, the variation seems to fall within the states defined here.



free (0) fused briefly at base (1) fused at least half way (2)

FIG. 2.23 STYLE FUSION

52. Style division (see fig. 2.24). Styles not divided (0); 2-lobed (1); 2 straight branches (2); 2 spiralling branches (3); lunate (4); lunate-bicornute (5); many branched (6). The form of the styles is very diverse. *Datisca* has styles which are very deeply divided into branches which are somewhat twisted; *Hillebrandia* and *B. meyeri-johannis* (sect.

Mezierea) have 5 styles which are each divided into 2 straight branches (bicornute); some species have spiralling branches e.g. *B. fischeri* and *B. acutifolia* (both sect. *Begonia*), *B. ulmifolia* (sect. *Donaldia*); while others have, what are described as lunate styles, e.g. *B. heracleifolia* (sect. *Gireoudia*). There is a lack of discontinuity between the states of lunate and bicornute, and instead of scoring the character as polymorphic or for the most common state, an extra state was described for the intermediate condition. When enough specimens were examined, a developmental series could be seen between the two states, and commonly the bicornute state developed from an extended growth of the ends of the lunate branches. Burt-Utley (1985) descibed this condition but did not describe it as a separate state. Both the American and Asian members of section *Knesebeckia* often have this intermediate state. It may be possible to delimit further states, for example the twice branching styles of *B. lobata* are quite squat in appearance, while some species, e.g. *B. wollnyi*, *B. uruapensis*, have somewhat longer branches; however enough evidence to make such further division has not been collected here.

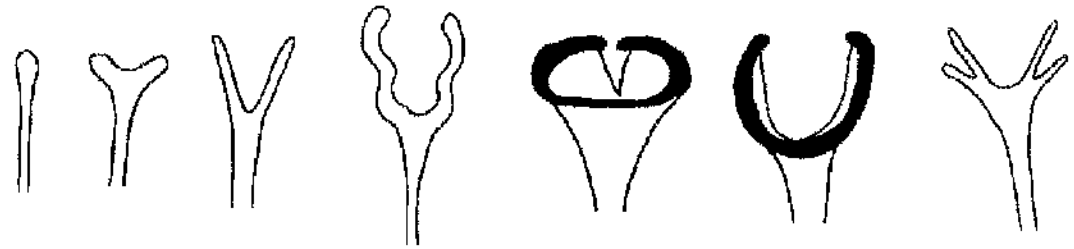


FIG. 2.24 STYLE DIVISION

53. Stigmatic tissue distribution (see fig. 2.25). Stigmatic tissue covering almost the entire surface of styles (0); covering entire surface, with some papillae confined to spiralling band (1); stigmatic papillae covering one side of style branch(es) (2); stigmatic papillae forming a band which encircles the style branch(es) (3) stigmatic papillae forming a band which spirals around the style branch(es) (4). The styles of *Datisca*, *B. acutifolia* (sect. *Begonia*) and *B. ulmifolia* (sect. *Donaldia*) are covered in papillose stigmatic material (state 0) but *B. ulmifolia* has some of the papillae confined to a spiralling band (state 1). The stigmatic band in *B. mannii* (sect. *Tetraphila*) is

confined to one side of the undivided style (state 2). The majority of *Begonia* have stigmatic papillose bands which encircle (state 3) or spiral around (state 4) the style branches.

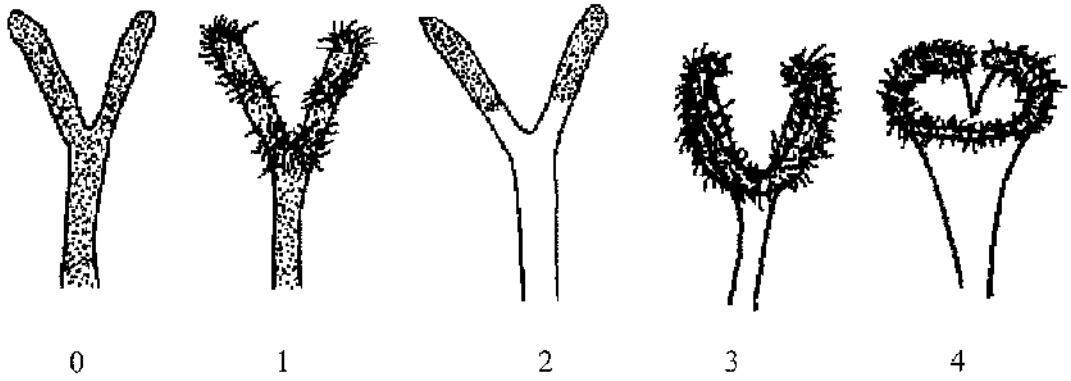


FIG. 2.25 DISTRIBUTION OF STIGMATIC PAPILLAE

2.2.2.5 FRUIT CHARACTERS

54. Persistence of female tepals on fruit. Female tepals persisting (0); deciduous (1). **55. Persistence of styles on fruit**. Styles persisting (0); deciduous (1). Like the longevity of the stipules and bracts, this apparently discontinous character is likely to be continuous in reality. Initially these two characters were scored as one multistate character, however this meant that those species with both persistent tepals and styles, e.g. *B. pedunculosa* and *B. franconis*, would not necessarily be grouped with species with persistent styles. One alternative to this would be to order the character but the development of these characaters is not known and thus ordering is rejected; I therefore described two characters. The American and Asian members of section *Knesebeckia*, with a few exceptions, have persistent styles. A. de Candolle (1859) and Irmscher (1925) have doubted the utility of this character as, in living material, the styles appear to fall off at variable times after the fruit reaches maturity but in the present study, it was felt that if enough specimens were observed, the character was useful.

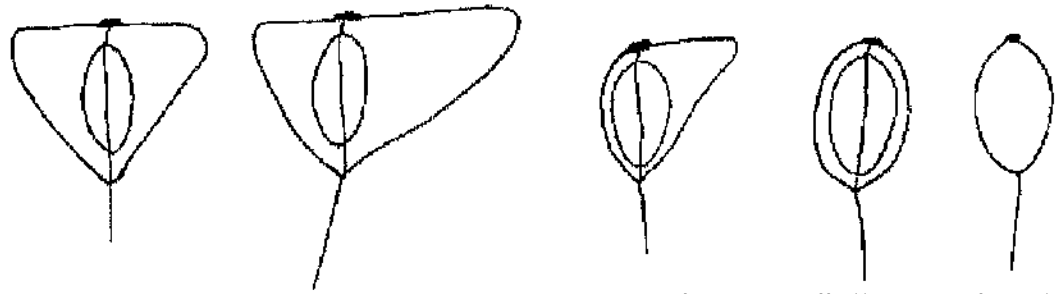
56. Fruit colour when dry. Evenly brown (0) capsule body dark brown, wings pale cream (1); evenly cream / white (2); green brown (3). This character has not been noted before. I observed that certain South American species, e.g. *B. glabra*, *B. convolvulacea*,

B. ulmifolia were distinguished by the occurrence of a very dark capsule body and pale cream wings, likewise, *B. olbia* and *B. hymenophylloides* and species in section *Coelocentrum* have very pale cream fruit bodies, while species with fleshy, leathery or paper-like fruits have green-brown coloured fruits when dried. The majority of *Begonia* species do not have any distinctive fruit colour when dry (evenly brown). Studies of fruit anatomy may shed light on this character.

57. Fruit capsule body wall. Fleshy or leathery (0); wood or shell consistency (1); paper-like (2); scarious (3). Only a few sections are characterised by fleshy or leathery fruits, i.e. *Mezierea*, *Tetraphila*, *Squamibegonia*, *Baccabegonia* and *Sphenanthera* with fleshy fruits (often appearing leathery when dry) and *Datisca* with chartaceous (leathery) fruits (cf. Clarke, 1879) and while sections *Loasibegonia* and *Scutobegonia* have somewhat fleshy fruit, they are described as paper-like here because the area covering the capsule body is very thin and translucent when fresh, appearing paper-like in dried material. This character is shared with sections *Lauchea*, *Monophyllon* and *Parvibegonia*. The majority of *Begonia* fruit are scarious. It was noted in the present study that some species have particularly rigid fruit which retain their structure when pressed, e.g. *B. pedata*, *B. biserrata*, *B. lobata*. Sosef (1994) also comments on the rigidity of the fruit capsules in section *Scutobegonia* and correlates this partly with the number of cell layers in the ovary wall, also suggesting that it may be due to greater induration of a layer bordering the locule cavity in the fruiting stage as, in one species (*B. scutulum* Hook.f.) the outer cells of this layer were sclerified, i.e. woody. Sosef, though, rejects this hypothesis and suggests that the reason may be the long length of time (6 months) that the fruit remain on the plant in *B. scutulum*.

58. Fruit wing presence and length (see fig. 2.26). Fruit wings ± equal (0); all wings, one longer (1); one long wing, the remainder ribs (2); ribs only (3); no wings or ribs present (4). Wing length is variable within species but falls discretely into the states described. Asian *Knesebeckia* all have one longer wing, while American *Knesebeckia*

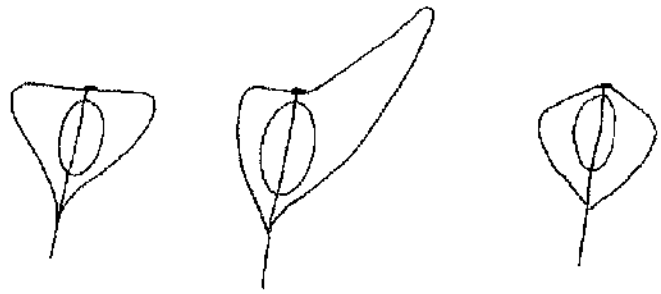
sometimes also have ± equal wings. Fleshy fruit often have no wings or ribs, and sometimes only ribs.



wings ± equal (0) | all wings, one longer (1) | one long wing, the remainder ribs (2) | all ribs (3) | no wings or ribs present (4)

FIG. 2.26 PRESENCE OF WINGS

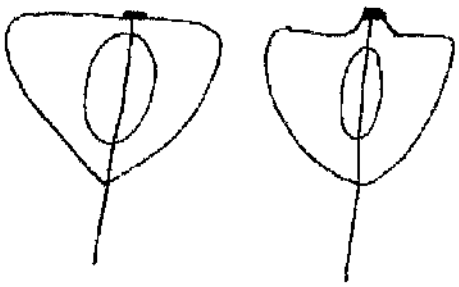
59. Fruit wing upper margin attitude (see fig. 2.27). Fruit wing upper margin horizontal (0); ascending (1); descending (2). The shape of wings in *Begonia* fruit is very variable, with the upper margin ascending or descending at quite different angles within one species. The upper margin is sometimes convex, but this was scored as horizontal here, as it is proposed that, this state could arise through the differentiation of cells along the top margin of the wing and this is distinct from the angle of wing.



horizontal | ascending | descending

FIG. 2.27 ATTITUDE OF UPPER MARGIN OF FRUIT WING

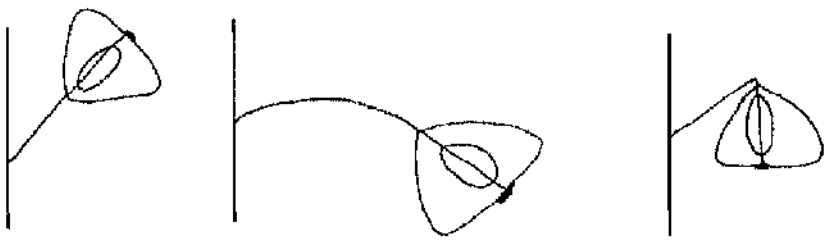
60. Fruit capsule apex (see fig. 2.28). Obtuse (0); acuminate - acute (1). A few species are distinguished by an acuminate apex, e.g. *B. oaxacana* agg. and species in section *Casparya* (not included here), and may be an adaptation involved in a pollination or fruit disperal syndrome.



obtuse (0) acuminate - acute (1)

FIG. 2.28 FRUIT CAPSULE APEX

61. Capsule pedicel attitude (see fig. 2.29). Capsule pedicel erect (0); pendulous (1); recurved (2). These character states arise after pollination. The majority of *Begonia* have pendulous fruit but some species have evolved erect or recurved fruit as probable adaptations for seed dispersal. The fleshy fruited African species have erect fruit, presumably for animal mediated dispersal, while many species in section *Platycentrum* are characterised by their recurved fruit, thought to be an adaptation for dispersal by rain (de Lange & Bouman, 1992).



erect (0) pendulous (1) recurved (2)

FIG. 2.29 ATTITUDE OF CAPSULE PEDICEL

62. Fruit dehiscence. Fruit indehiscent (0); dehiscing at margins of wings (1); dehiscing irregularly along back of capsule body (2); dehiscing in between styles (3). *Datisca* and *Hillebrandia* are distinguished by the dehiscence of their fruit beween their styles, a character associated with the development of the ovary and its inferior nature. Charpentier (1989b) found that all *Begonia* have open apices at a certain time during their development. Although the African fleshy fruited species have been scored as

indehiscent here, some have been shown to open like a banana unpeeling from the top, e.g. *B. loranthoides* (sect. *Tetraphila*) (see de Wilde & Arends, 1979, photo 1 p. 361) and this could be hypothesised to be an extension of the dehiscence shown by *Datisca* and *Hillebrandia*. The species in sections *Loasibegonia* and *Scutobegonia* have indehiscent fruit (Sosef, 1994).

2.2.2.6 SEED CHARACTERS

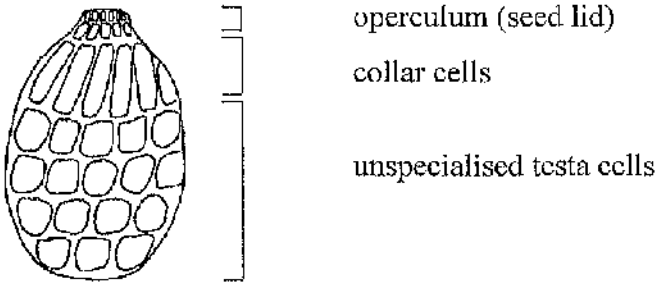


FIG. 2.30 ILLUSTRATION OF SEED CHARACTERS

63. Specialised testa cells (see fig. 2.30). Present (0); absent (1). The Begoniaceae is distinguished from the Datiscaceae by the presence of a ring of specialised testa cells below the seed lid called collar cells which have a function in germination (Bouman & de Lange, 1983).

64. Seed aril presence (see plate 21A, C, E or F, de Lange & Bouman, 1992). Present (0); absent (1). The seeds of section *Tetraphila* possess a large aril which is an autapomorphy.

65. Seed ornamentation presence (see fig. 2.30). Present (0); faint or absent (1). The African fleshy fruited species (not sections *Loasibegonia* and *Scutobegonia*) have a very much reduced or absent seed ornamentation (de Lange & Bouman, 1992). Some species in South America have also been noted with this reduction in ornamentation (Bouman & Badcock, unpublished data), e.g. *B. olbia*, *B. dichroa* and *B. oaxacana*, and although the majority of species with reduced ornamentation are from fleshy fruit, the South American species, *B. olbia* and *B. dichroa*, have scarious fruit and therefore this

character is not completely linked to fruit type. *B. oaxacana* has had multiple accessions examined for seed characters (Bouman, pers. comm.), and shows quite a range of variation in seed ornamentation which would urge caution; however, this species is part of a group of species / basionyms in need of revision (pers. ob.) and the variation observed may be correlated with taxonomy.

66. Seed operculum shape. Flat (0); nipple shaped (1); obtuse (2); columnar (3). The majority of *Begonia* species have nipple shaped opercula. *Dattsca* and *Hillebrandia* share a columnar seed operculum. The fleshy fruited African species, section *Coelocentrum*, *B. acutifolia* and *B. socotrana* have obtuse opercula.

2.2.2.7 EXCLUDED CHARACTERS AND CHARACTERS WITH POSSIBLE UTILITY FOR FUTURE INVESTIGATIONS

1. **Leaf nerve reticulation** (Sosef, 1994; Tebbitt, 1997; pers. obs.) (see plate 13b in Tebbitt, 1997). This character will probably be particularly useful in analyses including section *Platycentrum* but was not included here as I found it difficult to record consitently from herbarium material.

2. **Trichome and hair types**. The different types of trichomes and hairs in *Begonia* were not classified here any further than identifying two types of stellate hairs / trichomes. It was felt that the material available was insufficient to determine all the different indument types and living material is best for this purpose. Another problem with this group of characters is that one species possesses more than one type of trichome and questions of homology of type and location are more complicated than on first impressions; nevertheless, these characters are likely to be phylogenetically informative, e.g. many species in section *Platycentrum* can be identified as belonging to this section partly by the dense, coarse, red hair on their petioles. Sosef (1994) remarked that several species of section *Scutobegonia* show comb-like structures on their petioles which consist of several hairs situated in a row and with merged bases and that other species of *Begonia* share this character, e.g. *B. goegoensis* (sect. *Reichenheimia*). Bona

& Alquini (1995) have investigated the trichomes of *B. setosa* Klotzsch from South America.

3. **Stigmatic papillae**. Panda & de Wilde (1995) investigated the stigmatic papillae in the Begoniaceae following up Baranov's (1977) preliminary investigation but concluded that, in general, the characters described were not suitable for section delimitation. I had intended to test their conclusions within a cladistic framework but felt that the large amounts of missing data did not warrant the inclusion in my analysis. There may be a problem with character state delimitation due to the continuous nature of the states described by Panda & de Wilde, although this is not an insurmountable problem.

4. **Stems woody at base**. This character was included by Tebbitt (1997) and was included here in preliminary investigations; however, I excluded the character from my analysis as I found it difficult to score consitently, particularly with respect to plants with a rhizomatous habit. Within horticultural circles *Begonia* are classified by their habit, one group being the cane *Begonia*. These *Begonia* have upright stems which are woody at their base, e.g. *B. dipetala*, *B. incarnata*, *B. grandis*. Some species in South America display considerably woodiness, e.g. *B. digitata* (sect. *Scheidweileria*), which, in the Royal Botanic Garden, Edinburgh, reaches the height of the glasshouse, with a stem diameter of c. 10 cm. Carlquist (1985) studied the wood anatomy of four South American species of *Begonia* from sections *Scheidweileria*, *Ruizopavonia*, *Huszia* and *Gaerdtia* but while concluding that the wood anatomy shared many similarities with the Datiscaceae, particularly *Datisca*, no conclusions about relationships within *Begonia* were made. Lee (1974) studied the stem anatomy of *Begonia* and concluded that most of the variation in stem anatomy showed no discernable pattern, either taxonomic or geographic, but indicated that further investigations of the nodal anatomy, leaf traces and a more comprehensive study of the vascular elements would be desirable.

5. **Cystoliths**. The occurrence of cystoliths was not investigated during this study but Doorenbos (pers. comm.) suggests that it is likely to be useful in delimiting groups.

Fellerer (1892) records the presence, location and type of crystals present. Horner & Zindler-Frank (1982) use spectroradiography to identify these crystals.

6. **Anther shape**. The shape of anthers in *Begonia* is very variable but appears phylogenetically useful. This character, initially included in the analysis here, was excluded as, at this level of analysis in *Begonia*, it was decided that the states would require delimitation by morphometric analysis. The majority of anthers in the American *Knesebeckia* are small, much shorter than the filaments (see character 39), obovoid, with arcuate dehiscence (see character 38). *B. maynensis*, *B. microcarpa* and *B. wollnyi* shared much more subglobular, even smaller anthers, with dehiscence through straight slits at the sides of pollen sacs. The connective of *B. wollnyi* was extended. Species in section *Gireoudia* are described with oblong, oblong-elliptic or obovate anthers (Burt-Utley, 1985) but these tend to be larger than those described above in section *Knesebeckia* (pers. obs.) The anthers of *B. peltata* (sect. *Rachia* placed in synonymy of sect. *Knesebeckia* by Irmscher in 1960) were characteristic of section *Gireoudia*. The anthers of *B. mucronistipula* and *B. ludwigii* were similar (to each other), being larger (than American *Knesebeckia*), with extended connectives, dehiscence through long slits and oblong to oblong-elliptic in shape. The anthers of *B. incarnata* were distinguished from the rest of the American *Knesebeckia* by their elliptic shape and larger size. Although the anthers of *B. dichroa* were obovoid, they were very different from the rest of section *Knesebeckia* with the connective visible between the two anther sacs and extended to form a hood. The Asian species of *Knesebeckia* were partly distinguished from the American species by the form of their anthers, which were usually about the same length as the filaments, oblong-ellipsoid to obovoid, connectives not extended to extended into a broad tip and dehiscing usually through long slits down the length of the pollen sacs (*B. pedunculosa* was an exception to this, with dehiscence, like species in section *Parvibegonia*, by very short arcuate slits). Occasionally some Chinese species dehisce through arcuate slits. The diversity of shape and form in *Begonia* is diverse and it is possible that investigations like that of Tebbitt & MacIver (unpublished data, 1997),

studying the endothecium of anthers in Begoniaceae, will be a fruitful way to gain characters from the anthers.

7. **Fruit capsule body shape**. As with anther shape, this character was initially scored for inclusion in my analysis but the variation will require morphometric delimitation of states before becoming useful. This will probably require living material as the fruit is one of the most three dimensional characters in *Begonia*. Tebbitt (1997) was able to use fruit shape to delimit groups within his lower level analysis but rather than recognising the diversity in fruit shape of species with scarious fruit, simply classified all such species, included in his study, as having ovate-elliptical fruit; perhaps a doubtful homology?

8. **Connective visible between the pollen sacs.** This character only became apparent after the majority of the data matrix had been scored and so has not been included here. This character is not directly linked to character 37 as species with extended connective do not all have visible connective between the pollen sacs.

9. **Leaf margin outline** (leaf entire, lobed, palmate or pinnate). This character was scored for all the species here but was excluded from the analysis as it was not felt, admittedly *a priori*, to be phylogenetically informative.

10. **Stomatal groups**. It is possible that the distribution of stomata (either solitary or in clusters) may be phylogenetically useful. Cuerrier *et al.* (1990) included this character in their numerical taxonomic study of Begoniaceae using leaf characters. Hoover (1986) studied the ecological response of stomata in two Mexican species of *Begonia*. Neubauer & Beissler (1971) also investigated stomatal groups in *Begonia*.

1. Fibrous roots, no obvious storage organ (0); swollen storage roots (1); root tube
2. Acaulescent or shortly caulescent (0); stem not branching (1); stem branching (2).
3. Stipules caducous (0); deciduous (1); persistent (2); absent (3).
4. Stipules ovate-lanceolate / triangular-lanceolate / linear-lanceolate (0); oblong-ellipsoid (1); triangular-ovate (2); broadly ovate (3).
5. Stipules entire (0) fimbriate (1); dentate or dentate-fimbriate (2).
6. Stipule nerve excurrent (0); not excurrent (1).
7. Bulbils present (0); absent (1).
8. Leaf cauline (0); petiolate (1).
9. Leaf leathery, no (0); yes (1).
10. Leaf venation pinnate (0); palmate-pinnate (1).
11. Leaf peltate (0); cordate with basal lobes (1); cordate without basal lobes (2).
12. Ring of hairs or trichomes at the junction of the leaf with the petiole present (0); absent (1).
13. Stellate trichomes present (0); absent (1).
14. Stellate hairs present (0); absent (1).
15. Monoecious with bisexual inflorescences (0); monoecious with unisexual inflorescences (1); dioecious or androdioecious (2).
16. Inflorescence axillary (0); terminal (1).
17. Partial inflorescence branching pattern monochasial (0); dichasial (1).
18. Inflorescence branching ± symmetrical (0); asymmetrical (1).
19. Single flower - one dichotomy (0); between 2-3 dichotomies (1); > 3 dichotomies (2).
20. Peduncle absent or less than 1 cm in length (0); present (1); elongated (2).

TABLE 2.2 SUMMARY OF MORPHOLOGICAL CHARACTERS AND THEIR STATES

21. Bract like stipules present (0); absent (1).
22. Bracts caducous (0); deciduous (1); persistent (2).
23. Bracts at first branching point obovate (0); ovate to ovate-lanceolate (1); broadly ovate or obovate (2).
24. Bracts at first branching point forming cup (0); fused (1); patent (2).
25. Bracts at second and later branching points oblong-obovate (0); ovate to ovate-lanceolate (1); obovate (2); broadly ovate or obovate (3).
26. Bracts at base of ovary present (0); absent (1).
27. Bracts where no obvious dichotomy occurs present (0); absent (1).
28. Flower colour white or pink (0); yellow or orange (1).
29. Male sepals (outer whorl) 2 (0); 4-5 (1).
30. Male petals (inner whorl) 0 (0); 2 (1); 5 (2).
31. Male sepal outer surface hairy (0); glabrous (1).
32. Male sepal apex acute to acuminate (0); rounded (1).
33. Male sepal margin entire (0); dentate (1); fimbriate to dentate-fimbriate (2).
34. Receptacle flat or slightly raised (0); rounded or a torus (1).
35. Androphore symmetrical (0); asymmetrical (1).
36. Filaments free to base (0); fused briefly at base (1); free to base, but some fusion in centre of androphore (2); fused into a column, with filaments arising all the way up the column (3); fused at least half way into a column (4).
37. Connective not extended (0); extended to a tip (1); extended to a ledge (2).
38. Stamen dehiscencing by long straight slits down the middle of the pollen sac (0); arcuate slits (1); very short arcuate slits in upper part of pollen sac (2).
39. Anthers shorter than filaments (0); anthers and filaments about same length (1); anthers longer than filaments (2).
40. Ovary inferior (0); partially inferior (1).
41. Ovary locules 1 (0); 2 (1); 3 (2); 4 (3); 5-7 (4).

TABLE 2.2 CONTD.

42. At least one locule not developing fully (0); all locules developing fully (1).
43. Placentation parietal (0); axile (1).
44. Placentae per locule 1 (0); 2 free placentae (1).
45. Placentae almost as long as the locule (0); less than half the length of the locule (1).
46. Female tepals free (0); fused (1).
47. Female tepals 2 (0); 3 (1); 4 (2); 5 (3); 6 (4); 10 (5).
48. Female tepal apex acute - acuminate (0); rounded (1).
49. Female tepal margin entire (0); dentate (1); fimbriate or dentate-fimbriate (2).
50. Styles: 2 (0); 3 (1); 4 (2); 5 (3).
51. Styles free (0); fused at base (1); fused for more than half their length (2).
52. Styles not divided (0); 2-lobed (1); 2 straight branches (2); 2 spiralling branches (3); lunate (4); lunate-bicornute (5); many branched (6).
53. Stigmatic tissue covering almost the entire surface of styles (0); covering entire surface, with some papillae confined to spiralling band (1); stigmatic papillae covering one side of style branch(es) (2); stigmatic papillae forming a band which encircles the style branch(es) (3) stigmatic papillae forming a band which spirals around the style branch(es) (4).
54. Female tepals persisting (0); deciduous (1).
55. Styles persisting (0); deciduous (1).
56. Fruit colour when dry evenly brown (0); capsule body dark brown, wings pale cream (1); evenly cream / white (2); green brown (3).
57. Fruit capsule body wall fleshy or leathery (0); wood or shell consistency (1); paper-like (2); scarious (3).
58. Fruit wings ± equal (0); all wings, one longer (1); one long wing, the remainder ribs (2); ribs only (3); no wings or ribs present (4).
59. Fruit wing upper margin horizontal (0); ascending (1); descending (2).

TABLE 2.2 CONTD.

60. Fruit capsule apex obtuse (0); acuminate - acute (1).
61. Capsule pedicel erect (0); pendulous (1); recurved (2).
62. Fruit indehiscent (0); dehiscing at margins of wings (1); dehiscing irregularly along back of capsule body (2); dehiscing between styles (3).
63. Specialised testa cells present (0); absent (1).
64. Seed aril present (0); absent (1).
65. Seed ornamentation present (0); faint or absent (1).
66. Seed operculum flat (0); nipple shaped (1); obtuse (2); columnar (3).

TABLE 2.2 CONTD.

3.2.3 ANALYSIS DETAILS

The data matrix (86 terminal taxa, 66 binary and multistate characters) (see table 2.3) was analysed using PAUP* 4.0d60 (Swofford, in prep.). Parsimony analyses were performed with heuristic searches using 50 replicates of random addtion sequence starting from random trees, followed by TBR branch swapping with all the most parsimonious trees saved (MULPARS "on"). Preliminary searches showed that there were several large islands of trees longer than the shortest tree and in order to save time, no more than 100 trees of score (length) greater than or equal to 702 were saved in each replicate. Only 50 replicates of random addition sequence, rather than the more currently cited 100 replicates (e.g. Steane *et al.* 1997), were used due to the size of the data matrix and the need to use the same searching options when calculating Bremer support values. Bremer support values (B. Bremer, 1996; K. Bremer, 1988; 1994;) were calculated by constructing constraint trees in TreeView (Page, 1996b), pasting these into NEXUS TREES and using these in PAUP* with the search options described above, except that no constraint was made on the number of trees to be saved over a given length. The support values were then calculated by subtracting the tree lengths found for each constraint tree from the original shortest tree length (700). To reduce the amount of time necessary for the analysis, only values for the major clades were calculated. The bootstrap (Felsenstein, 1985) was not used because morphological data sets [especially]

are thought to deviate strongly from the ideal of random samples (Sanderson, 1995); the bootstrap assumes an initial round of random sampling of characters from some postulated universe of characters (Sanderson, 1995).

```
[                                10        20        30        40        50        60        ]
[                                .         .         .         .         .         .         ]

B._acerifolia                    0222001101 1111001022 1012171001 1100020100 2111003171 1531001210 110171
B._alicida                       0122111101 1111011121 0212210001 1100041220 1111003771 2431173020 210177
B._angustiloba                   2123010011 2111011001 0210711001 1100040100 2111003001 1241003000 110171
B._annulata                      4220101111 1111001011 1120711001 0000032010 2011007771 1541177121 210177
B._ascendens                     70777777211 1111701012 1112111077 7777777770 2111001771 1131003110 110101
B._asperifolia                   3002011101 1111011112 0120111001 1100040010 2111003101 0431003110 110171
B._balmisiana                    2122010011 1111011011 0210111001 0110040100 2111003101 1531003210 110101
B._biserrata                     0202211101 2111101011 1012111001 0020040100 2111003021 1241001100 110101
B._boissieri                     2102011101 1011011011 1121301001 1111040100 2111703111 154100???? ??0171
B._brevirimosa                   4210011171 1111101021 1112101000 1100030120 2111003101 124??03000 110171
B._bulbillifera                  2123210001 1111011000 1230711001 1010040110 2111003001 1531003120 110101
B._convolvulacea                 ?2000?1101 1111?01021 1012111001 1101101020 2110?03??1 1301113200 110177
B._cordifolia                    1010071101 1111001021 1212170001 1100010200 2111003??1 253000227? 100177
B._crenata                       010?010101 1111011121 1100210001 1000141220 1111?03000 2430032127 220171
B._cuernavensis                  0110010101 1111011001 1220711001 1010040100 2111?03011 2241003170 177177
B._dealbata                      2123210001 1111011000 1110711001 1010040100 2111?03001 1431003100 110177
B._dichroa                       0212011111 1111001021 1222301101 1101002100 2111003101 024??????? ??0111
B._dipetala                      0210011101 1111001021 1020177000 1100010010 2110100101 1241103020 110177
B._dregei                        3222010101 1111001011 1120311000 1000001000 2110003071 2241003027 110101
B._falciloba                     ??00211101 1011001111 1012301001 1020040100 2111003021 2341003100 110101
B._fernaldiana                   2?10011101 1111011011 0122271001 1000040100 2111003001 1541003120 110171
B._fimbristipula                 3002111101 1111011112 0012111001 1100040000 2111001101 1241003100 110171
B._floccifera                    4020001111 1111001021 1212110000 1??0040010 2110002071 1530003027 110177
B._franconis                     7102111101 1110011001 1012110001 1101031000 2110103001 0230003020 110177
B._gemmipara                     1102010101 1111011011 7110107077 7777777770 2110?03?70 1410003110 100107
B._googoensis                    4020001111 0111001022 107?110001 7107077777 2110001101 124??03020 110177
B._gracilis                      2112210101 1111011001 0230711001 1010040110 2111003001 1241003100 110101
B._grandis_subsp._grandis        3110010101 1111011111 0120211001 1100040010 2111007101 1241003110 110101
B._grandis_subsp._holostyla      3110010101 1111011111 0120111001 1100040120 2111002101 1431003110 110171
B._heracleifolia                 4020001101 1011001122 1122301000 1100102120 2111000101 243?103100 110171
B._hintoniana                    2200111111 1111011021 ?012111001 0011000100 2111?03011 1531001??0 1?0171
B._ignea                         2223210101 1011011011 0122311001 0021030100 2111003021 1541103020 110101
```

TABLE 2.3 MORPHOLOGICAL DATA MATRIX

B._imperialis	400???1101	1110001011	112?111000	0100041020	1111100070	2431101120	210???	
B._incarnata	0210001101	1111001021	1012111001	1000040020	2111003001	2531003100	110?71	
B._johnstonii	0212010101	1011001011	1112171701	1??0000000	2111003??1	2241003107	110101	
B._josephi	3012210101	0111011112	0112111001	0100141020	2111003101	1431003110	110?71	
B._labordei	3002011101	1111011112	1012111001	1000140020	2111002101	1431003110	110101	
B._lobata	?2000?1101	1111?01021	1012111091	0001001020	2110103??1	1231011200	110171	
B._ludwigii	?220011101	1011001122	1110101001	1100001000	2117003101	154???????	??0101	
B._malachosticta	4210001171	1111101021	1112101000	1100030120	2111003101	124??03000	110?71	
B._mannii	0200011110	11??101000	1122?11001	0100042020	3101002102	1021130471	000012	
B._martabanica	0102110101	1111011121	0112110001	1070041220	1111003000	2431172121	220171	
B._mascniana	4017011101	1111001122	1112110001	0100040020	2101001101	1241023100	210172	
B._maynensis	0120001110	2111001021	1212111001	1001010100	2111103001	0541003000	110101	
B._meyeri-johannis	0200011101	1101101011	1022111000	1100002000	4101?07103	1241130471	000112	
B._michoacana	2?10211101	1111011001	0012?11001	0021040100	?1?1?03021	1431077777	??0177	
B._microcarpa	0220001111	1111001021	1012101001	1000020000	?1????3001	0531103000	210171	
B._modestiflora	1110210101	1111011021	0112110001	0000141020	2111003001	1431103110	110101	
B._nemoralis	??00211101	1?11101011	10???11001	0120040100	?1???03021	124???????	??0177	
B._novo-granatae	4000001101	1111011112	1022??1010	0001030100	?1???02102	0621103??0	??0177	
B._oaxacana	0200011101	1011001011	1120?11001	0120000100	21???01101	1241130321	100111	
B._obliqua	?220001111	1011001011	1012?01001	1000101020	2111103001	2301103100	110172	
B._olbia	?110011101	2011001020	1222210001	1100000100	2111103011	1541123020	110111	
B._palmata	4200001111	1111001011	1020111001	0100032000	2011003??1	1541171121	210177	
B._pedata	?102211001	2111011010	0022311001	0110040100	2111003011	1241001020	110101	
B._pedunculosa	3112211100	1111011011	1212111001	1100140210	2111003101	1430003110	110101	
B._peltata	4020001111	0111001122	1012111001	0100000110	2111001101	1531003000	110101	
B._picta	3010211101	1101011011	1110111001	0120031010	2111003121	1241003110	110101	
B._poculifera	0200011111	2101007011	1220301000	0100111020	3101000102	1511130471	100112	
B._portillana	2112211101	1011011111	1220311001	0020020100	2111003001	1531073100	110171	
B._prismatocarpa	4000211101	1101000001	1212?11100	0100140020	3110000102	2431132371	000101	
B._prolifera	3000211101	1111011121	1102217001	1100041020	1111?02000	2430032121	220177	
B._putii	3112217101	1111011111	0122111001	0100040020	2111002101	243??0310?	110177	
B._quadrialata	4002211101	0111000011	1212101100	0100140020	3110000122	1431132371	000101	
B._rajah	4020001171	1111?01112	1112111000	1100040020	2110070101	2241103020	110177	
B._rhodochlamys	??10211101	1111001121	1112111001	1021040100	?1???03001	1531003121	110171	
B._roxburghii	4200011111	1111201010	1012117001	0100001000	3111002102	1241130477	100171	

TABLE 2.3 CONTD.

B._rubella	1000012101	1111011122	1112111001	1100041020	2111001101	1241003110	1101??
B._salaziensis	0200011111	1101001011	1012111001	1100011020	210??02101	1241130420	000111
B._sandtii	2112210101	1111011001	1230?11001	1120040110	2111?03001	1531003100	110101
B._satrapis	3012011101	1111011012	1110110001	0120001000	2111003121	1541??????	??01??
B._sericoneura	4020001111	1111001022	1122?01000	1100101110	2111000101	2531103100	1101?1
B._socotrana	30220?0101	0111001021	122?210001	1101000010	2110003101	1240003120	110102
B._sutherlandii	0222210101	1011001011	1112111101	1100011000	2111003101	2241103100	110101
B._tayabensis	4010111111	0111001022	1020311001	11000?1??0	2111003??1	????103101	210171
B._tenera	4020001101	1111001011	1210110001	0100001010	2110003??1	1431173021	1101??
B._ulmifolia	?200001110	2111?01021	1212111000	0101001010	2111003??1	1311013200	110171
B._uniflora	2110210101	1011001001	1220?11001	1100020100	2111003101	1531003100	110171
B._uruapensis	2120000101	1111011011	0112111001	1001000100	2111003001	1?41003320	110171
B._verticillata	0102010101	1111011121	110?210001	?000040?20	1111?02000	1430032121	2201??
B._weberlingii	2110210101	1011?01001	1?12??1001	101002??0?	?1?????????	??????????	??01??
B._wilsonii	3010011101	1111011112	1102111001	1000100010	2111?01101	0431002320	1?0101
B._wollnyi	2220001101	1111001022	1212111007	1100001000	2111003001	0240003000	110101
Datisca_cannabina	42?????100	211120?000	0???????0?0	1?00000021	2101107??1	0301130470	131103
Hillebrandia_sandwicensis	?222011101	101107?021	1220301012	1??1001021	4101005003	0241003470	?30103
Symbegonia_sanguinea	4210001171	1111101071	1112111000	0000031120	2111013001	124??03000	110171

TABLE 2.3 CONTD.

2.3 RESULTS

Three characters were parsimony-uninformative. The analysis resulted in 5340 equally most parsimonious cladograms (TL = 700, CI = 0.1714, RI = 0.5497, RC = 0.0942). These trees were contained in two islands (see Maddison, 1991), the first containing 4476 trees, the second containing 863 trees. The results of the search for islands of equally parsimonious are given in table 2.4. Different islands of trees of equal length may present different hypotheses of character evolution (Maddison, 1991) and I have therefore presented a strict consensus (with bootstrap values and decay indices) (fig. 2.31) and an Adams consensus (fig. 2.32) for all the most parsimonious trees, a strict (fig. 2.33) and Adams (fig. 2.34) consensus tree for the most parsimonious trees in island 1 and a strict (fig. 2.35) and Adams (fig. 2.36) consensus tree for the most parsimonious trees in island 2. One of the most parsimonious trees, arbitrarily chosen, is also illustrated as a phylogram, to show relative branch lengths (fig. 2.37).

Island	Size	First tree	Last tree	Score	First replicate	Times hit
1	4476	1	4476	700	43	1
2	864	4477	5340	700	48	1
3	468			701	30	1
4	100!			702	2	4*
5	100!			703	20	7*
6	12			703	22	1
7	100!			704	5	5*
8	100!			705	3	6*
9	100!			706	1	6*
10	100!			707	9	6*
11	100!			708	14	2*
12	100!			709	4	4*
13	100!			710	8	2*
14	100!			711	19	3*
15	100!			713	37	1

! Islands with a size of 100 equally parsimonious trees will most likely be larger than this as searches which found trees longer than 702 were aborted when 100 trees were found. This was to reduce computation time.

* Multiple hits on islands of unsaved trees may in fact represent different islands.

TABLE 2.4 TREE-ISLAND PROFILE OF MORPHOLOGICAL DATA SET FOR 86 TAXA

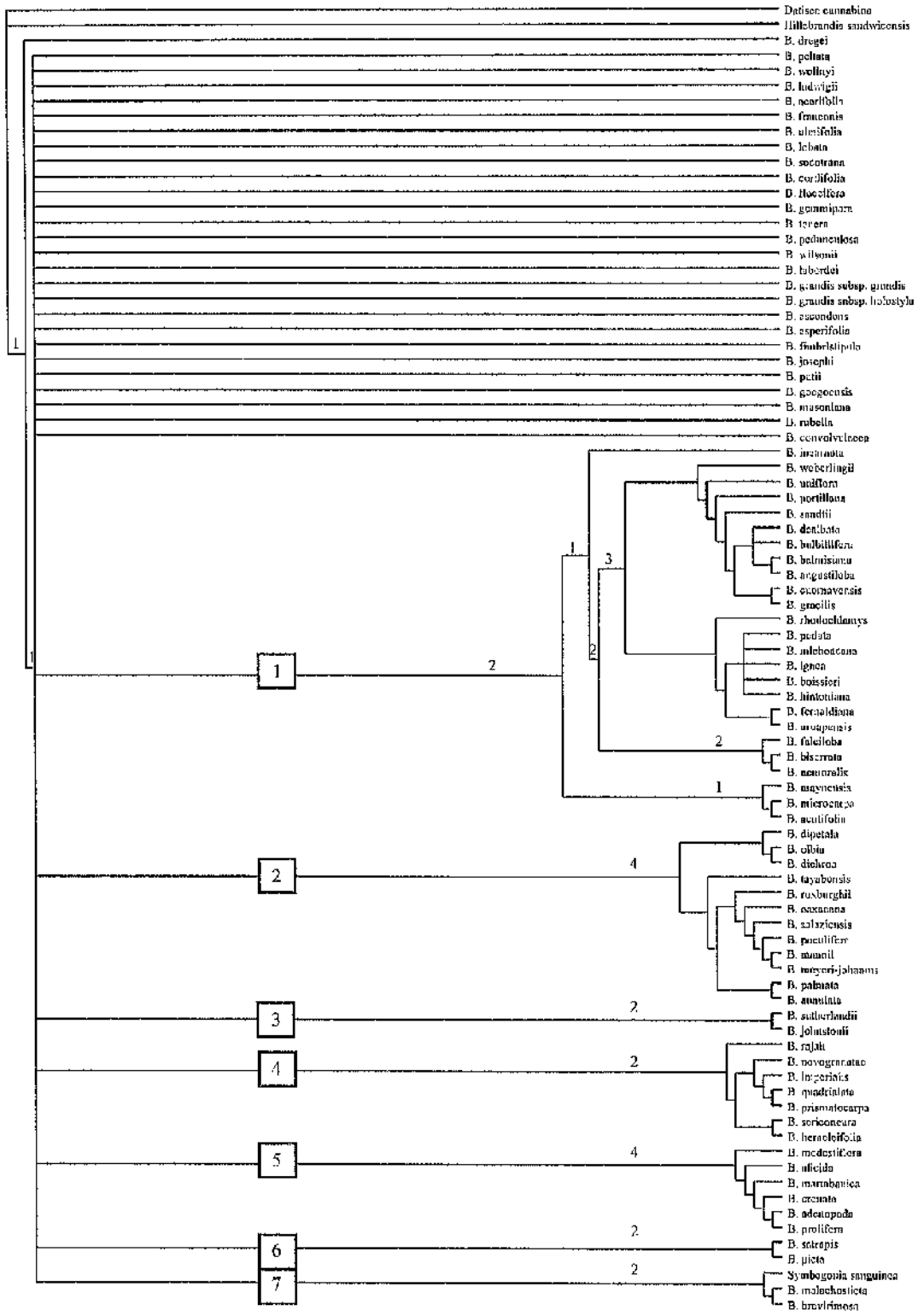


FIG. 2.31 STRICT CONSENSUS OF 5340 EQUALLY MOST PARSIMONIOUS TREES OF 700 STEPS (CI = 0.1714, RI = 0.5497). NUMBERS ABOVE THE INTERNODES ARE DECAY INDICES. BOXED NUMBERS ARE CLADE MARKERS.

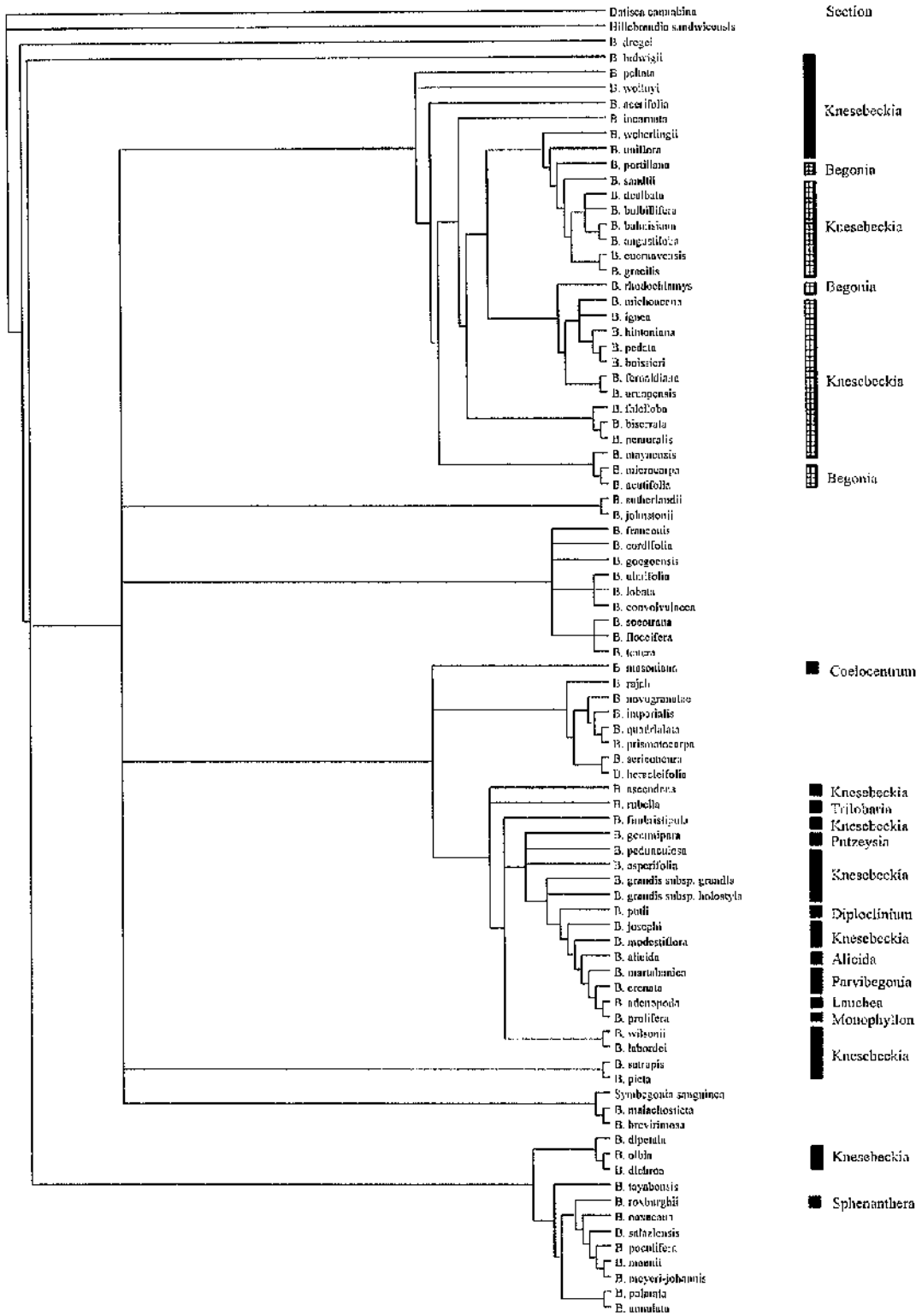


FIG. 2.32 ADAMS CONSENSUS OF 5340 EQUALLY MOST PARSIMONIOUS TREES OF 700 STEPS (CI = 0.1714, RI = 0.5497). SHADED BLOCKS = ASIA; CROSS-HATCHED BLOCKS = AMERICA

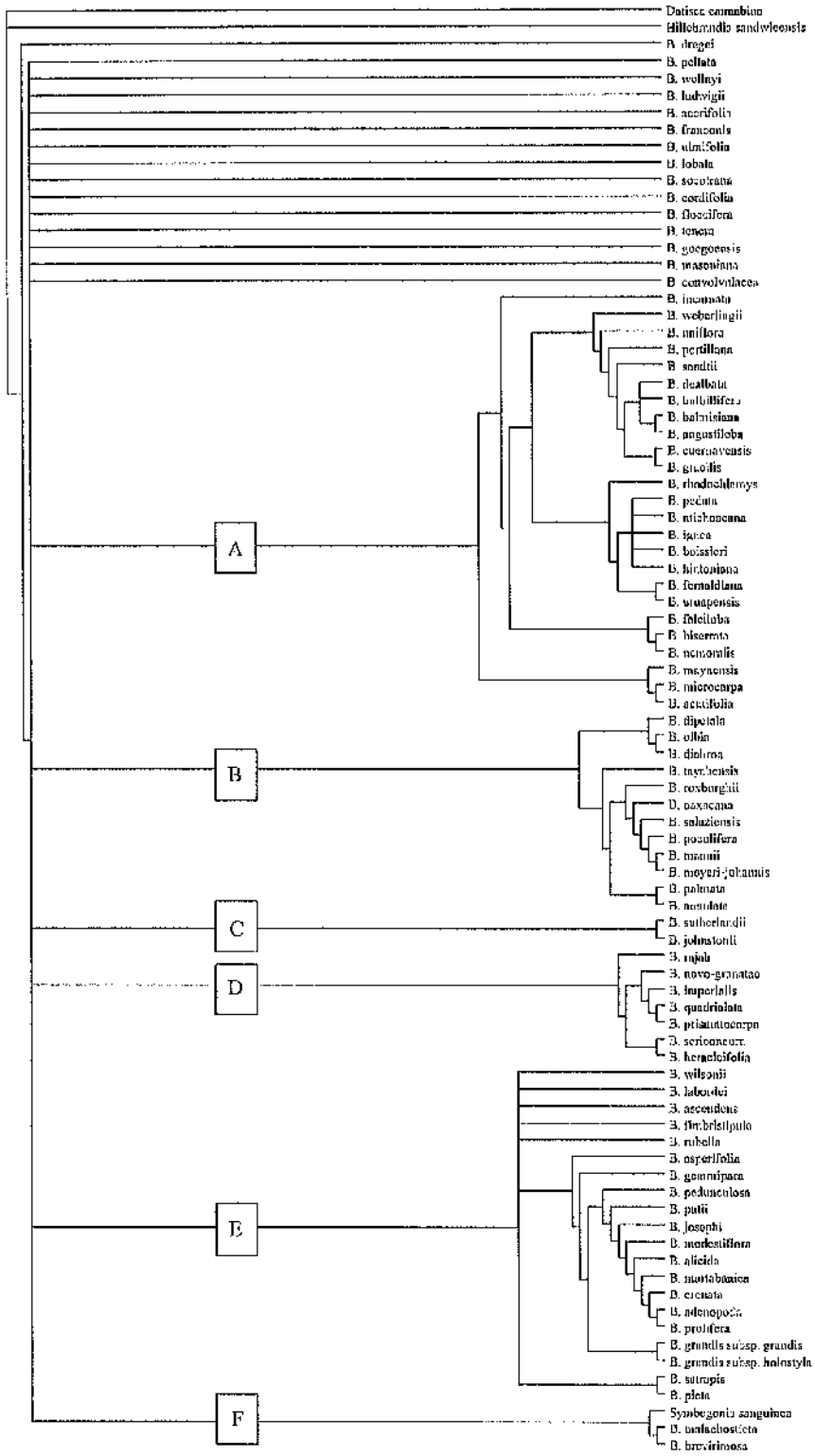


FIG 2.33 ISLAND 1: STRICT CONSENSUS OF 4476 EQUALLY MOST PARSIMONIOUS TREES OF 700 STEPS (CI = 0.1714, RI = 0.5497).

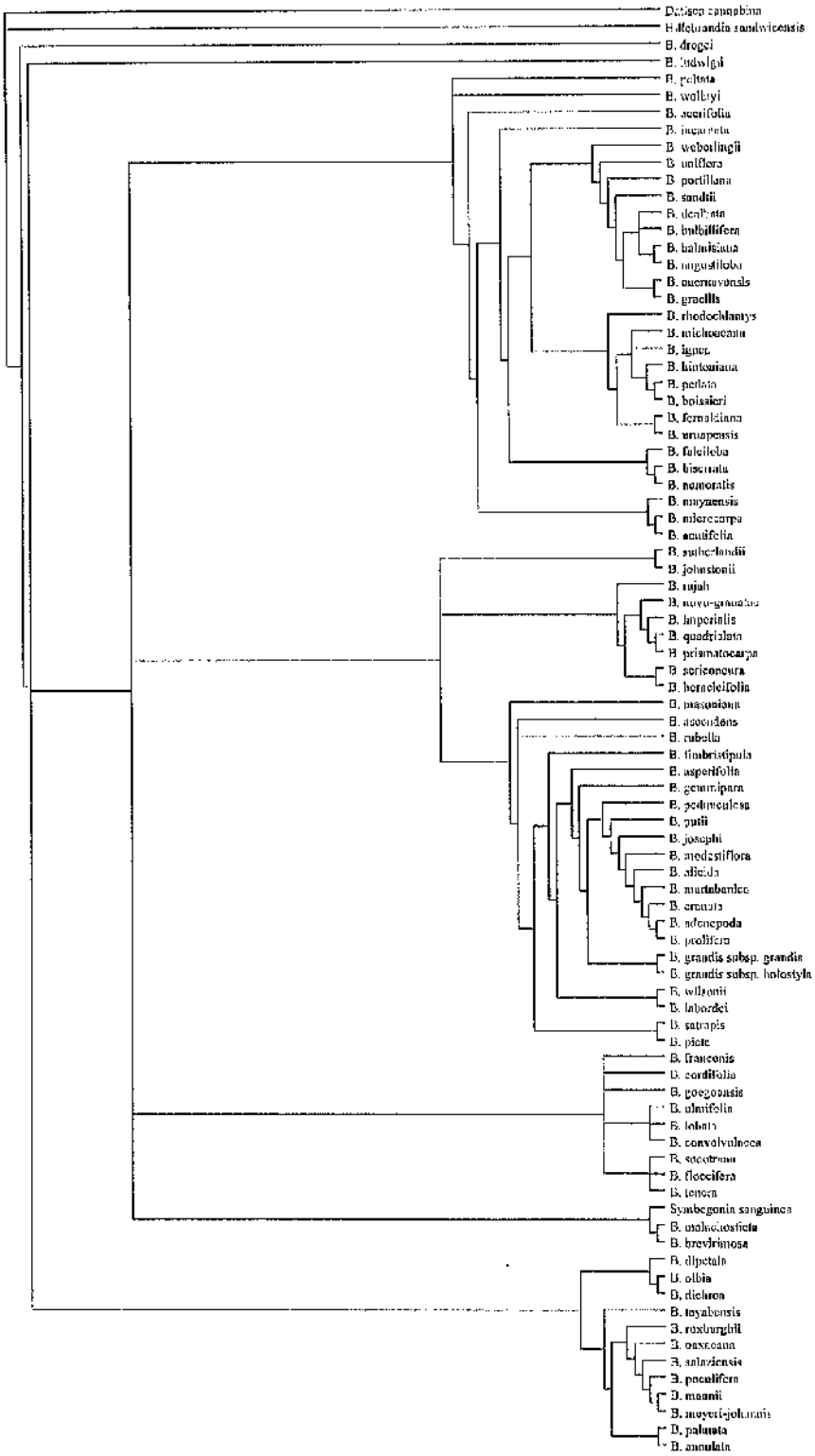


FIG. 2.34 ISLAND 1: ADAMS CONSENSUS OF 4476 EQUALLY MOST PARSIMONIOUS TREES OF 700 STEPS (CI = 0.1714, RI = 0.5497).

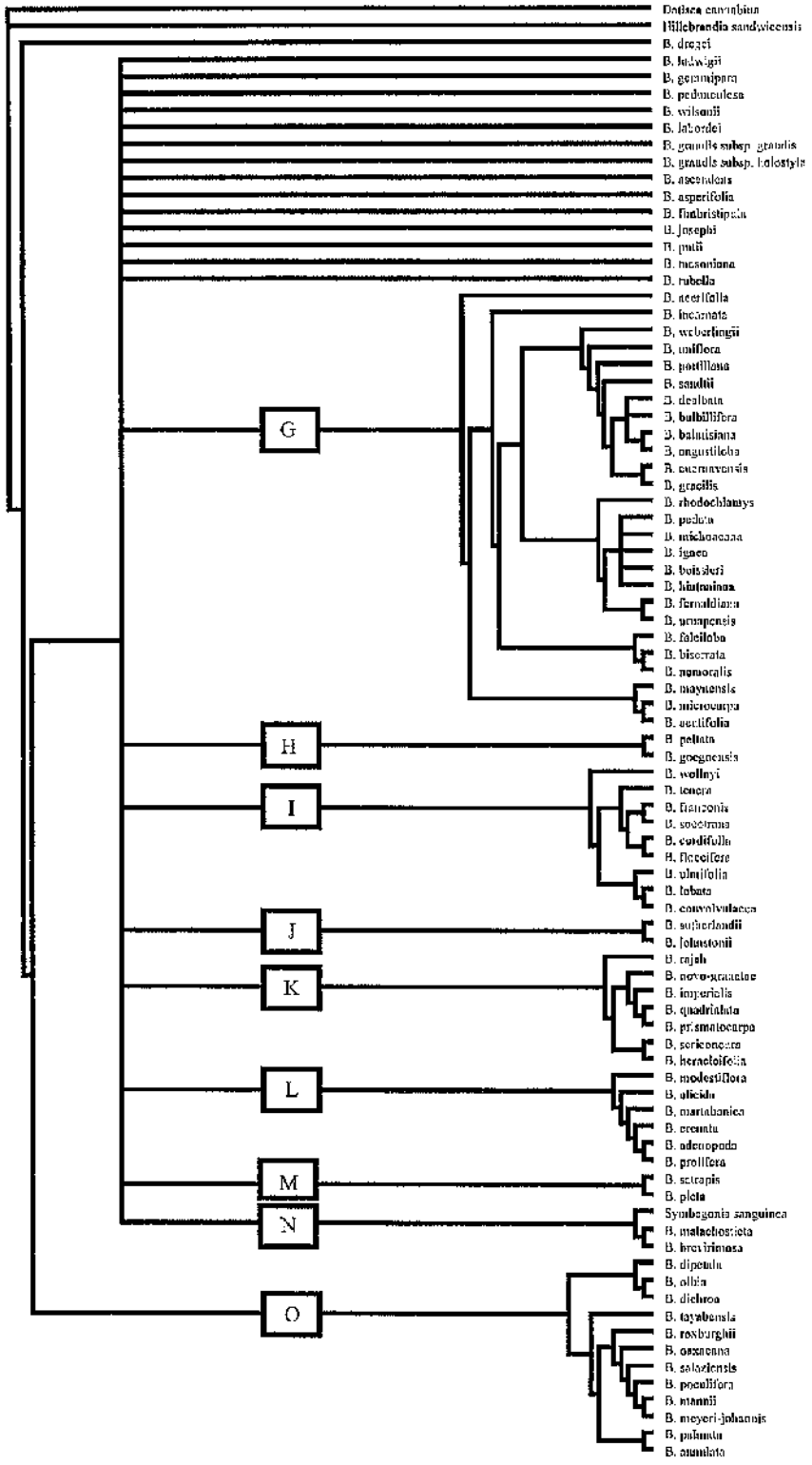


FIG. 2.35 ISLAND 2: STRICT CONSENSUS OF 863 EQUALLY MOST PARSIMONIOUS TREES OF 700 STEPS (CI = 0.1714, RI = 0.5497).

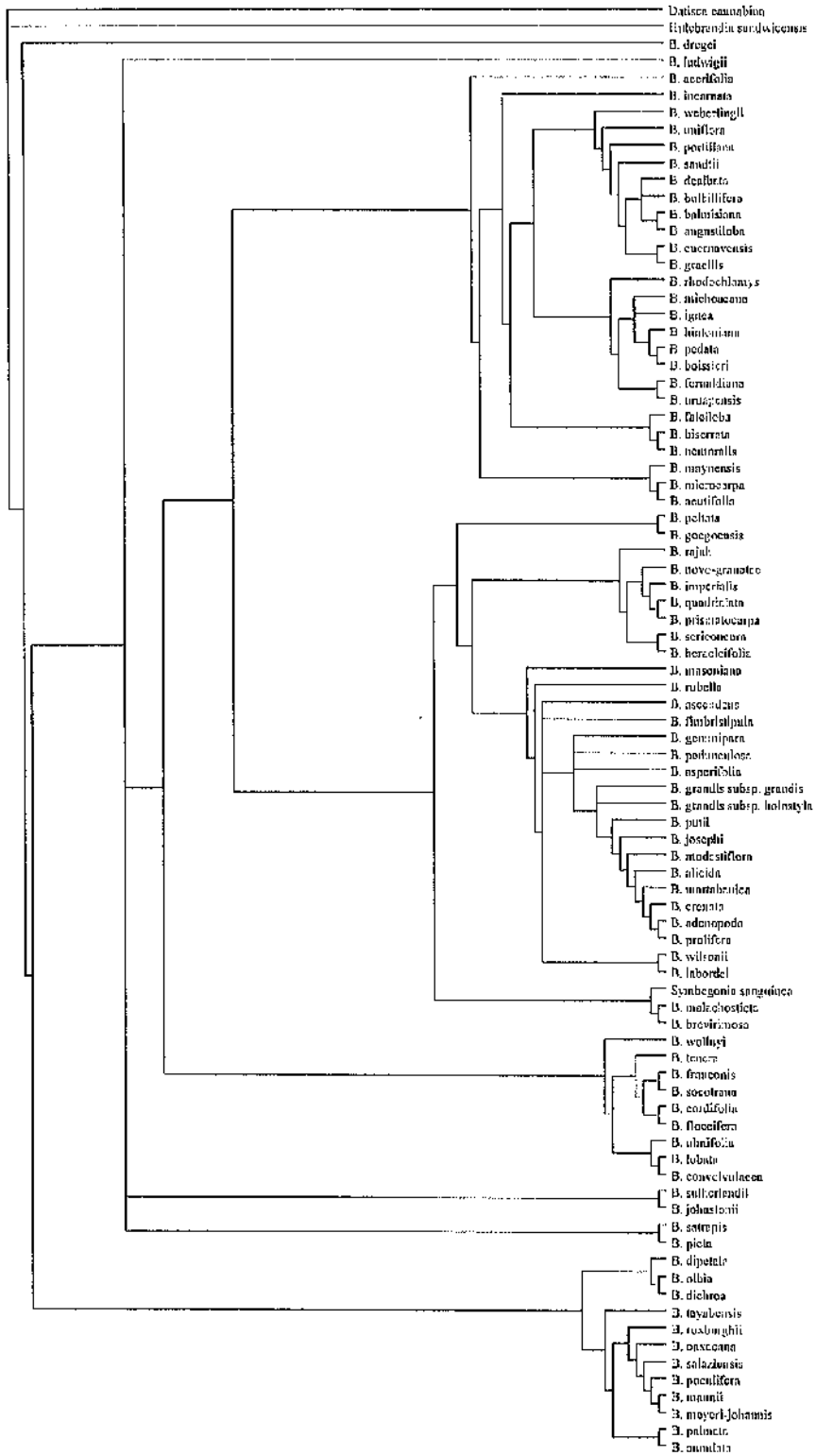


FIG. 2.36 ISLAND 2: ADAMS CONSENSUS OF 863 EQUALLY MOST PARSIMONIOUS TREES OF 700 STEPS (CI = 0.1714, RI = 0.5497).

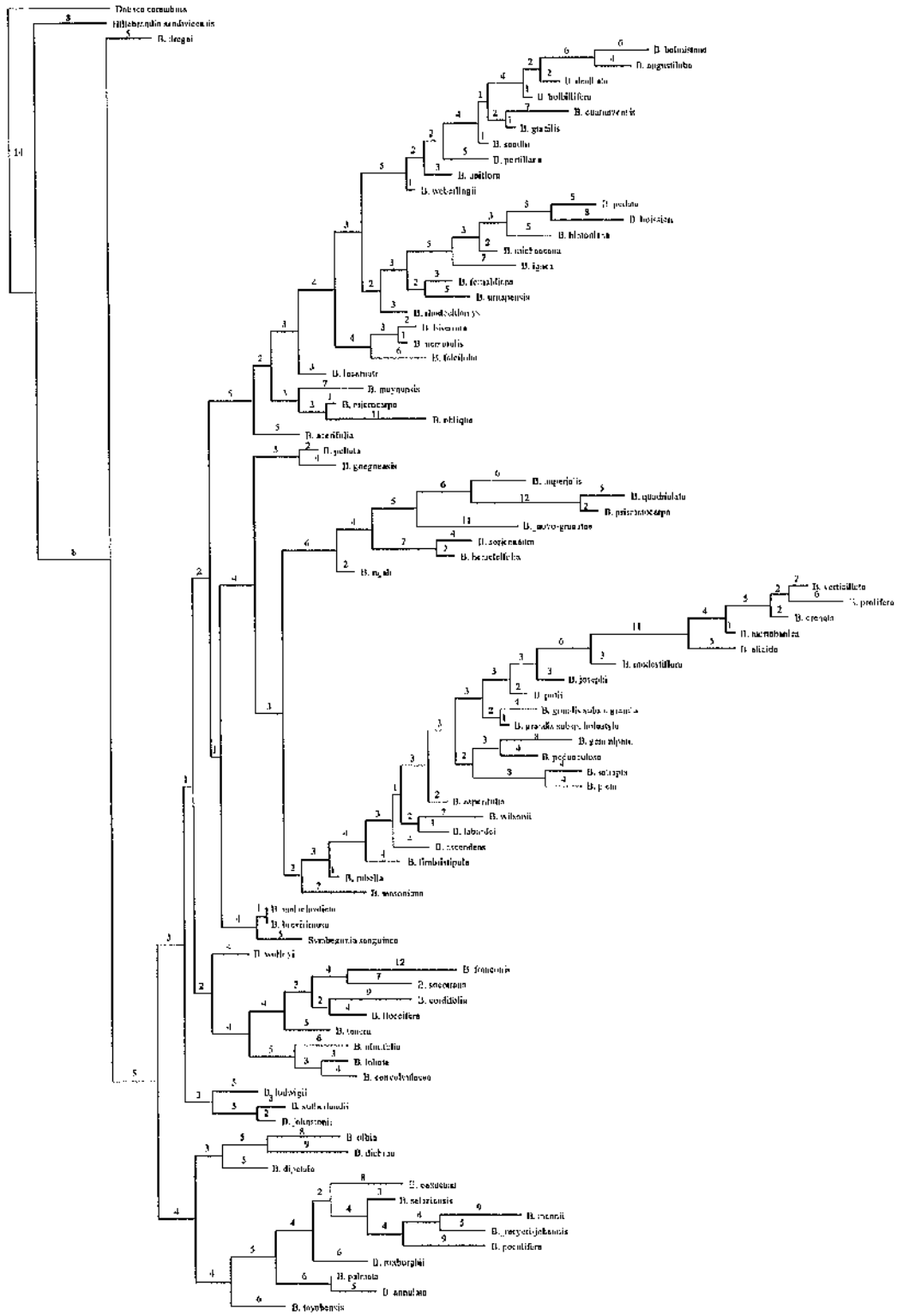


FIG. 2.37 ONE OF 5340 EQUALLY MOST PARSIMONIOUS TREES OF 700 STEPS (CI = 0.1714, RI = 0.5497). THE NUMBER OF SUPPORTING CHARACTER STATE TRANSFORMATIONS INFERRED FROM ACCTRAN OPTIMIZATION IS GIVEN BELOW THE BRANCH. BRANCH LENGTHS ARE PROPORTIONAL TO THE AMOUNT OF CHANGE OCCURRING ALONG THEM.

The consistensy index (CI) and retention index (RI) for the data set are low, 0.1714 and 0.5497 respectively. This is not unexpected with a morphology data set of this size, for example Liede (1997) presented a morphological study of 79 African members of *Cynanchum* (Apocynaceae - Asclepiadoideae) and the CI for this data set was 0.181 and the RI was 0.468. Givnish & Sytsma (1997) investigated the likelihood of correct phylogenetic inference in relation to the amount of homoplasy in a data set. Homoplasy was represented by the CI and they showed that if the CI was low and the number of independent, variable characters was high, the likelihood of correct phylogenetic inference was "moderate", while if the number of independent, variable characters was high, the likelihood of correct phylogenetic inference was "low". In relation to the present investigation, this would suggest caution when interpreting the results of the analysis.

The strict consensus of all the trees (fig. 2.31) illustrates the clades that are always present in both islands of most parsimonious trees. *Hillebrandia* appears at the base of the tree with the outgroup, *Datisca*, and *Begonia* forms a monophyletic clade; *B. dregei* occurs at the base of this clade. Within the large clade of *Begonia* there are seven major clades, each unresolved with respect to each other. Clade 1 contains the majority of American *Knesebeckia* with *B. acutifolia*, *B. microcarpa*, *B. portillana* and *B. rhodochlamys* from section *Begonia*. *B. acutifolia* is very similar to *B. obliqua*, the type of *Begonia*, and this would suggest that the boundaries of these two sections require revision. Clade 2 contains species from *Asia*, *America* and *Africa*. *B. olbia* and *B. dichroa*, placed in section *Knesebeckia* by Barkley & Golding (1974), are placed as a sister group to *B. dipetala* (sect. *Haagea*). Within this clade there is a clade containing species with fleshy, indehiscent fruit (*B. roxburghii* - *B. meyeri-johannis*) and species in sect. *Platycentrum* form a sister clade to these species. Clade 3 contains two species from sect. *Rostrobegonia*. Clade 4 also contains species from America, Asia and Africa with species from sections *Reichenheimia*, *Gireoudia*, *Hydristyles*, *Weilbachia* and *Loasibegonia*. *B. modestiflora* (Asian *Knesebeckia*) is basal within clade 5 to species

from sections *Alicida*, *Lauchea*, *Monophyllon* and *Parvibegonia*. Clade 6 contains 2 Asian *Knesebeckia* which represent two putative sister species. Clarke (1879) previously recognised this close relationship. Clade 7 is notable because it indicates the paraphyletic nature of *Begonia*, suggesting that the genus *Symbegonia* and section *Petermannia* are sister groups.

Adams consensus trees place taxa at the most resolved node common to all trees. The problem with this consensus method is that it can produce monophyletic groups that are not amongst the set of most parsimonious trees. In the Adams consensus tree of all the most parsimonious trees (fig. 2.32), clade 1 in the strict consensus tree is expanded to include the rest of the American *Knesebeckia* scored in this analysis. This clade still contains species from section *Begonia*. The Asian *Knesebeckia* which were unresolved in the strict consensus tree form a monophyletic clade with the taxa from clade 5. The main difference in the Adams tree is the positions of clade 2, which, together with *B. ludwigii*, is separated from the main clade of *Begonia* to form a trichotomy.

The majority of clades are present in the strict consensus trees of both islands. Clade A is present in both clades with the addition of *B. acerifolia* in island 2. Clade E, which contains the Asian *Knesebeckia* in island 1, is unresolved for these taxa in island 2. Clade H and I in island 2 are unresolved in island 1. The main difference between the structure of the strict consensus trees in islands 1 and 2 is the position of clade B in island 1 and the equivalent clade, O, in island 2. This clade, containing the indehiscent, fleshy fruited species with parietal placentation from Africa appears as the sister group to the rest of *Begonia* (except *B. dregei*).

2.4 DISCUSSION

The tree island profile (table 2.4), the CI, RI and low decay indices all indicate that the tree space for the morphological data presented here is relatively flat with several almost equally parsimonious tree islands. This means that there are several almost equally viable evolutionary hypotheses for this data set. It is therefore difficult to draw many

strong conclusions about the evolution of *Begonia*. The results discussed here are taken from the Adams consensus tree of all 5340 equally most parsimonious trees of 700 steps long. The Adams consensus tree was used because it provides an almost fully resolved tree representing the "best" consensus of both islands of trees.

2.4.1 THE MONOPHYLY OF SECTION *KNESEBECKIA*

All the consensus trees indicate that *Knesebeckia* is not monophyletic; in fact, when a constraint tree was constructed to force the group to be monophyletic, the tree was 8 steps longer. As well as these results showing that the Asian and American species should not be included in the same group, *B. olbia* and *B. dichroa* are also indicated as not being closely related to the remaining species currently included in the section.

2.4.2 SOUTH AMERICAN *KNESEBECKIA*

The South American species *B. olbia* and *B. dichroa* take an unusual position within the phylogeny presented here, forming a clade with *B. dipetala*, an Indian and Sri Lankan cane *Begonia*, which, together, are sister to a clade containing mostly African and Asian species from sections *Diploclinium*, *Platycentrum*, *Sphenanthera*, *Hexaptera*, *Mezierea*, *Squamibegonia* and *Tetraphila*. This sister clade contains some species with fleshy indehiscent fruit. *B. olbia*, *B. dichroa* and *B. dipetala* are all anemophillous (wind dispersed) species, with relatively large fruit that have wings more or less equal in length. These species are woody. The fruit of *B. olbia* and *B. dichroa* dry to a pale almost creamy colour and the placentae in *B. olbia* are less than half the length of the locule. This character combination has also been observed in a rare herbaceous Burmese species, *B. hymenophylloides* Airey-Shaw ex L.B.Sm. & B.G.Schub. Although interesting, these South American species do not appear to require consideration in the context of a future systematic study of *Knesebeckia sensu stricto*.

2.4.3 CENTRAL AMERICAN *KNESEBECKIA*: INTRASECTIONAL RELATIONSHIPS

The strict and Adams consensus trees for all the trees are almost identical. The strict consensus clade, supported by a decay value of 2, contains species from sect. *Knesebeckia* and sect. *Begonia*.

Doorenbos (pers. comm.) suggests that that within this core of taxa I have sampled, the species can be separated into two sections. The group containing *B. incarnata*, the type of sect. *Knesebeckia*, would contain mainly South American species with shortly rhizomatous roots, branching stems, and axillary inflorescences. The second group would be based around *B. boissieri* (=*B. abaculoides* Ziesenh.) for which Ziesenheine (1968) created the section *Quadriperigonia* Ziesenh. and which is currently a synonym of *Knesebeckia*. This group would contain mainly Mexican species with tubers, axillary bulbils and thyrsoid inflorescences (racemes made up of cymose partial inflorescences). Along with *B. incarnata*, Doorenbos includes (as sampled here) *B. acerifolia*, *B. cuernavacensis*, *B. fernaldiana*, *B. falciloba*, *B. hintoniana*, *B. ignea*, *B. incarnata*, *B. ludwigii*, *B. maynensis*, *B. michoacana*, *B. microcarpa*, *B. nemoralis*, *B. olbia*, *B. uniflora*, *B. weberlingii* and *B. wollnyi*. In the *Quadriperigonia* group, Doorenbos includes (as sampled here), *B. angustiloba*, *B. balmisiana*, *B. biserrata*, *B. boissieri*, *B. bulbillifera*, *B. dealbata*, *B. gracilis*, *B. pedata*, *B. portillana*, *B. rhodochlamys*, *B. sandtii* and *B. uruapensis*.

These groups only partially agree with the trees presented here. *B. acutifolia* was used in this analysis rather than *B. obliqua*, due to the greater availability of material and their very similar morphology. If the assumption is correct and *B. acutifolia* represents a species very similar to the type of sect. *Begonia*, *B. maynensis* and *B. microcarpa*, which occur in a clade together with *B. acutifolia*, may be better represented in sect. *Begonia*. These species are all woody, rhizomatous - fibrously rooted, have lanceolate-triangular stipules with excurrent nerves and a pair of bracteoles at the base of the ovary. The anthers of *B. microcarpa* and *B. maynensis* are distictively small, subglobular and

dehiscing along their sides. The styles of *B. acutifolia* are distinctive with spiralling branches and the papillose surface distributed all over the styles.

The clade containing *B. falciloba*, *B. biserrata* and *B. nemoralis* is distinguished by the fact that all three species have one-sex inflorescences, borne in separate leaf axils. These species are also shortly rhizomatous, upwardly branching, somewhat woody subshrubs with cymose inflorescences.

The next large clade, supported by a decay index of 3, contains species with root tubers, except *B. cuernavacensis* (and this species looks like it may form a very small tuber if necessary but there was only limited material to examine here). The rooting system of *B. rhodochlamys* was not seen, and *B. pedata* was scored as missing data as both tuber and short rhizomes were observed. During the course of the present study, a large number of specimens were seen for this group of *Begonia*. It was found that the species limits of *B. gracilis* require revision. At present, for *B. gracilis*, there are seven varieties recognised, including the typical variety, and the ranks of *B. cuernavacensis*, *B. sandtii*, *B. bulbillifera*, and *B. dealbata* need considering in the context of any revision of *B. gracilis*. *B. dealbata* has the appearance of a poor form of *B. bulbillifera*. (A new taxon in this *gracilis* group was also discovered.) With chromosome counts of 2n = 28 and 2n = 56 in this group (Legro & Doorenbos, 1969; 1971), an approach combining population genetic studies and cytology would seem appropriate. This clade contains the species which Doorenbos refers to as possessing thrysoid inflorescences, but the clade also contains taxa with single flowered inflorescences. There are trends in this clade for taxa to have broadly ovate stipules and a compressed / reduced peduncle (see characters 2 & 20).

2.4.4 CENTRAL AMERICAN *KNESEBECKIA*: INTERSECTIONAL RELATIONSHIPS

Three taxa are placed at the base of this clade of American "*Knesebeckia*" in the Adams consensus tree, indicating their "floating" position in this analysis. These taxa are *B.*

peltata, *B. wollnyi* and *B. acerifolia*. Although *B. ludwigii* was, somewhat suprisingly, not included here, being unresolved at the base of the main *Begonia* clade, it shares several significant character states with these taxa, i.e. an upright rhizomatous habit, persistent, ovate-lanceolate stipules and an extended peduncle. *B. ludwigii* also has a fused ring of trichomes at the junction between the petiole and leaf. *B. peltata* has, for a long time, been postulated as intermediate between sections *Gireoudia* and *Knesebeckia*; its taxonomic history reflects this. Klotzsch placed this species in his genus *Rachia* Kl. which de Candolle demoted to a section of *Begonia*; Warburg (1894) placed *Rachia* as a subsection of sect. *Magnusia* (now a synonym of sect. *Gireoudia*) as did Irmscher in 1925 but in 1960, Irmscher moved *B. peltata* to sect. *Knesebeckia*; Barkley & Baranov (1972) placed the species in sect. *Gireoudia* and then Baranov & Barkley (1974) replaced *B. peltata* in sect. *Knesebeckia*. This chequered taxonomic history reflects the intermediary position of *B. peltata* between sect.s *Knesebeckia* and *Gireoudia*. With the characters described above, oblong anthers and three female tepals, *B. peltata* shares many character states with *Gireoudia*. While Burt-Utley (1985) mentioned this situation, she did not attempt to validate *B. peltata*'s inclusion in *Knesebeckia*. Although avoiding such a chequered history, probably through rarity, *B. ludwigii* also appears to have strong affinities with *Gireoudia*.

In this analysis *Gireoudia* is located in a clade with sections *Weilbachia*, *Hydristyles*, *Reichenheimia* (Asian), *Loasibegonia* and *Scutobegonia* (African). The occurrence of the Asian and African sections together with the American sections, in this particular instance seems anomalous and would seem to be based on a number of convergent characters, e.g. growth habit, tepal number. Burt-Utley (1985) believed that *Weilbachia* was closely allied to *Gireoudia* due to similarities in growth forms, blade form, villous to squamose induments and apetalous flowers. De Candolle (1864) associated *Gireoudia* with *Knesebeckia*, an opinion shared by Doorenbos (pers. comm.) and myself. All three of these Central American sections share a chromosome number of 2n = 28. It would seem that there is a lot of room for improvement in the cladistic analysis of *Begonia* morphology above the section level.

2.4.5 ASIAN *KNESEBECKIA* INTERSECTIONAL RELATIONSHIPS

The strict consensus of all the most parsimonious trees provides no resolution for the Asian *Knesebeckia*, except *B. modestiflora*. This reflects the uncertain position of these species within the entire phylogeny and not their lack of integrity as a clade or even the branching pattern within the clade of Asian *Knesebeckia*. The Adams consensus of all the trees appears to reflect a reasonable hypothesis for these taxa which is not contradicted by the strict consensus of islands 1 or 2.

One immediate conclusion from this analysis is that the Asian *Knesebeckia* are paraphyletic with *B. rubella* (sect. *Trilobaria*), *B. gemmipara* (sect. *Putzeysia*), *B. putii* (sect. *Diploclinium*), *B. alicida* (sect. *Alicida*), *B. martabanica* and *B. crenata* (sect. *Parvibegonia*), *B. adenopoda* (sect. *Lauchea*) and *B. prolifera* (sect. *Monophyllon*) being nested within the Asian *Knesebeckia*. This agrees with Irmscher's (1929) hypothesis that, within Asia, *Knesebeckia* represents a primitive type in terms of flower and habit characters, with more "advanced" flower and habit types being derived from this primitive type.

To unravel this complex clade it is helpful to view a phylogram of one most parsimonious tree (see fig. 2.37). The branch lengths to *B. gemmipara* and to *B. modestiflora* (or to *B. alicida*, depending where you draw your line) are relatively long, reflecting their morphological distinctness. *B. gemmipara* is a very distinctive species possessing a unique form of bulbil (see character 7), seeds which are among the largest found in *Begonia* (Bouman & de Lange, 1983) and an unusual, unidentified waxy substance in which the seeds are embedded in the capsule (pers. obs.). These characters warrant the maintanance of the monotypic section *Putzeysia* for this species. From my experience of the morphology of sections *Alicida*, *Parvibegonia*, *Lauchea* and *Monophyllon*, these species form a well supported monophyletic group which may be best treated as one section. In any future revision of these species, all four of these sections would need to be studied together. It is likely that *B. modestiflora* resembles the

hypothetical ancestor of this clade. Although not included here, *B. surculigera* Kurz from Burma and *B. minicarpa* Hara from Nepal probably also belong here along with *B. modestiflora*, intermediate between the Asian *Knesebeckia* and the *Parvibegonia* group.

2.4.6 PARAPHYLETIC HIGHER TAXA

The implication of this pattern of evolution is not uncommon in plants: a large, diverse, wide-ranging group, with morphologically distinct, monophyletic groups evolving from within the group, making the large group paraphyletic. *Streptocarpus* has recently been shown to be paraphyletic with respect to *Saintpaulia* (Möller & Cronk, 1997) and there are many examples of island radiations of distinct species groups from continental progenitors, e.g. Darwin's finches (see Givnish, 1997) and the Hawaiian Silverswords (see Baldwin, 1997). Many would argue that this, in a phylogenetic system of classification, should mean that the monophyletic derivative group should be "sunk" into the larger group to prevent the occurrence of paraphyletic taxa (an extension of the phylogenetic species concept); however, in this particular instance, this would mean the loss of a morphologically distinct group with a good deal of information content and I would not advocate this course of action, even after a more thorough investigation has been undertaken.

2.4.7 RELATIONSHIPS WITH SECTION *DIPLOCLINIUM*

To return to the clade of Asian *Knesebeckia*, *B. rubella* (sect. *Trilobaria*) and *B. putii* (sect. *Diploclinium*) were also found to nest within *Knesebeckia*. In these cases, the species are not morphologically distinct from the Asian *Knesebeckia*. When trying to discuss other researchers hypotheses for sect. *Diploclinium*, the situation is complicated by the fact that section *Diploclinium sensu* Irmscher is polyphyletic. When Jin & Wang (1994) referred to *Diploclinium* they used *B. peltatifolia* Li and *B. wangii* T.T.Yu as examples, summarising the section's morphology as axile, bilamelate (simple at base) placentation, 3 carpels, 3 locules, 3 winged capsule and herbaceous with stems modified to rhizomes or stems short, thick and borne on rhizomes. This is probably a common

perception of what section *Diploclinium* is, as it more or less reflects Irmscher's (1925) circumscription of the section; however, when a list is made of species currently included in *Diploclinium* (Barkley & Golding, 1974), the species are very diverse (pers. obs.; Doorenbos, pers. comm.), including tuberous and rhizomatous species, glabrous and densely hairy species, 2-3 locular ovaries, tepal numbers in the female flower of 3-5 and 2-4 in the male flower, subglobose - oblong anthers and free or fused styles and anthers. Within the analysis presented here, *B. cordifolia* and *B. tayabensis* are also representatives of section *Diploclinium*. These species represent two very different morphologies; *B. cordifolia* is a delicate, tuberous herb from Sri Lanka and India while *B. tayabensis* is a robust, thickly rhizomatous herb from the Philippines. It is plausible that *B. tayabensis* represents the lineage that Jin & Wang (1994) refer to. From the present analysis there is no evidence to support Jin & Wang's evolutionary hypotheses but this is only a preliminary attempt at a phylogenetic analysis of *Begonia*, and molecular sequencing studies (Badcock, unpublished data; see fig. 3.9) combined with morphological data may support their proposals.

In future analyses of the Asian *Knesebeckia* it will be necessary to include species from sections *Trilobaria* and *Diploclinium* (see chapter 4). It is unlikely that *Trilobaria* represents a well defined group of species as two taxa, *B. dioica* and *B. laguensis* Elmer, examined for their seed morphology (Bouman, pers. comm.) appear distinct from the taxon included here (see chapter 4). *B. putii* is representative of a group of species, currently included in *Diploclinium*, from the IndoChina region which were described mainly by Craib in 1930. These species with distinctive fused staminal columns, occur in the northern areas of IndoChina.

2.4.8 ANSWERING PREVIOUS EVOLUTIONARY HYPOTHESES

Several of the initial questions posed in the introduction can be quickly assessed now. The evidence is not conclusive with respect to the relationships of *B. grandis* and *B. modestiflora* or *B. labordei* and *B. fimbristipula*; neither is it conclusive with regards to

the possible hybrid origin of *B. labordei*, *B. fimbristipula* and *B. wilsonii*. To answer these questions, particularly the latter, it will probably be more fruitful to look for different sources of evidence, e.g. cytology and molecular data. There is certainly evidence to show that the acaulescent habit is polyphyletic and within the Asian *Knesebeckia*, acaulescence appears to be basal but the pattern is not clear cut. With respect to the replacement of *Knesebeckia* by *Petermannia* in the south, there is no evidence to support this in an evolutionary sense.

2.4.9 TOWARDS A PHYLOGENY OF *BEGONIA*

Several of the analyses (Adams consensus of all trees and strict consensus of island 2 trees) do indicate that a clade containing the African fleshy fruited species occurs at the base of the *Begonia* phylogeny, however, this clade does not form the ultimate basal clade, which is *B. dregei*. This result is both unexpected and unexplained. A major problem with the analysis of *Begonia* morphology is the choice of *Datisca* as an outgroup. Although there is little doubt that *Datisca* is the sister group to the Begoniaceae (see ref.s cited earlier, paragraph 1.1), sharing seed, carpel and stamen characters, many features of *Begonia* and *Datisca* morphology have diverged. *Datisca* has a reduced or absent perianth, stipules and bracts and many of the flower characters important in *Begonia* are obviously adapted for wind pollination in *Datisca*. This means that polarizing the analysis with *Datisca* as the outgroup may swamp any characters which are conservative and potentially useful in reflecting the true phylogeny of *Begonia*. Similarly, de Lange and Bouman (1992) have commented that *Mezierea* possesses many characters which are derived, reflecting the species' zoochorous seed dispersal and this could therefore confound attempts to construct a phylogenetic analysis of the Begoniaceae using *Datisca* as an outgroup. I am therefore refraining from drawing any conclusions about the phylogeny of *Begonia* based upon this analysis of *Begonia*. I would also agree with de Lange and Bouman (1992) that any speculation as to the centre of origin of *Begonia*, is, as yet, pure conjecture. Instead I advocate the use

of a data set independent of morphology to test these ideas about the evolution of *Begonia*.

2.5 CONCLUSIONS

A phylogenetic analysis of the Begoniaceae has not been published before and as such this is a first attempt at a morphological analysis of the family. While I have shown that using morphology to reconstruct a phylogeny of *Begonia* is fraught with difficulties, it is without doubt useful within sections and closely related sections to study character evolution and aid classification. I have shown that *Begonia* section *Knesebeckia* is not monophyletic and is, in fact, polyphyletic. The Asian *Knesebeckia* should actually to be referred to as section *Diploclinium*, the type of the section being *B. grandis*. As an aid to future taxonomic studies of these taxa I have tried to indicate which species groups will need to be investigated together with the taxa already allocated to section *Knesebeckia*. In addition to this foundation work for future revisions, I have also investigated previous evolutionary hypotheses for sect. *Knesebeckia* and the genus *Begonia*.

CHAPTER 3: THE UTILITY OF THE NONCODING CHLOROPLAST DNA REGION *TRN*C - *TRN*D TO PRODUCE A PHYLOGENY OF *BEGONIA* L. AND HOW IT COMPARES WITH MORPHOLOGICAL DATA

3.1 INTRODUCTION

There is no published phylogeny for *Begonia* L. The accepted classification of *Begonia* follows Irmscher (1925) and divides Begoniaceae into 3 genera, and *Begonia* into c. 80 sections of which all except one, section *Knesebeckia* (Klotzsch) A.DC., occur on only one continent. Irmscher (1925), and before him, Warburg (1894), grouped the sections according to the continent upon which they occur; however, there is no comment from either author as to whether this reflects their ideas of evolutionary relationships or if this was simply a utilitarian choice.

There are two published cladistic studies of three African sections, *Scutobegonia* and *Loasibegonia* (Sosef, 1994) and *Mezierea* (Klazenga *et al.*, 1994), one study proposing evolutionary relationships based on evidence from the study of the ovaries of some Chinese *Begonia* (Jin & Wang, 1994) and one unpublished cladistic study of section *Sphenanthera* (Hassk.) Benth. & Hook.f. *sensu* Barkley & Golding, 1974 (Tebbitt, 1997). Several studies have commented on the close relationships of the African sections *Mezierea*, *Squamibegonia*, *Baccabegonia* and *Tetraphila* (Arends, 1985; de Wilde, 1985; Van den Berg, 1985; Reitsma, 1984; 1985; de Lange & Bouman, 1985; 1992) and the primitive status of *Mezierea* among African *Begonia* (e.g. Arends, 1985; de Wilde, 1985; de Wilde & Arends, 1989; Reitsma, 1984; 1985; Van den Berg, 1985; Klazenga *et al.*, 1994). All these studies, with the exception of Tebbitt (1997), are based exclusively on morphological data and despite covering only a fraction of the genus, represent the only explicit hypotheses of phylogenetic relationships within *Begonia*. There is therefore an urgent need for a phylogenetic framework in *Begonia*.

During the course of research to investigate the phylogenetic basis of sect. *Knesebeckia*, it was necessary to produce a preliminary estimate of the phylogeny of *Begonia* in order to test the monophyly of *Knesebeckia*; both molecular and morphological data sets were produced for this purpose and the data sets were investigated for their degree of congruence.

3.1.1 MORPHOLOGICAL DATA

A cladistic analysis of the morphology of *Begonia* is presented in chapter 2 and the reader is referred to this for a discussion of the characters used by previous authors to suggest evolutionary hypotheses in *Begonia*.

3.1.2 MOLECULAR DATA

In collaboration with Mark Tebbitt, a pilot study of sequence variation in the chloroplast *trn*L intron (see Gruissem, 1989; Clegg *et al.* 1991) and the intergenic spacer between *trn*L and *trn*F failed to find sufficient variation to resolve relationships amongst 12 species of *Begonia* (chosen to sample the morphological variation and distribution of the genus) (Tebbitt, 1997; Badcock & Tebbitt, unpublished results). Tebbitt (1997) subsequently investigated the variation in four chloroplast intergenic regions and one mitochondrial intron by restriction enzyme digests of PCR products (PCR RFLPs). The primers used were those designed by Demesure *et al.* (1995) and are part of a set of universal primers now available (also see Taberlet *et al.*, 1991; Dumolin-Lapegue *et al.*, 1997; Strand *et al.*, 1997) In total, Tebbitt surveyed c. 11 Kb (length estimates from data on the European *Quercus robur* complex by Demesure *et al.*, 1995, as data not given by Tebbitt, 1997) of the estimated 170 Kb chloroplast genome of *Begonia* (Palmer, unpublished data, cited in Downie & Palmer, 1992). This research discovered that the noncoding region *trn*C [tRNA-Cys (GCA)] - *trn*D [tRNA-Asp (GUC)] of the chloroplast genome might contain sufficient variation to warrant sequencing studies for phylogeny reconstruction in *Begonia*. A subset of the *trn*C - *trn*D RFLP data generated

by Tebbitt (1997) is included in appendix L and an analysis of this data is compared with the sequence data presented here, in paragraph 3.3.2.3.

The *trn*C - *trn*D intergenic region is located in the large single copy region of the chloroplast which is characterised by a higher substitution rate than the inverted repeat region (Wolfe *et al.*, 1987). Transfer RNA genes are highly conserved enabling the design of universally applicable primers (Demesure *et al.*, 1995) and the amplification of spacer regions between the genes.

Data from noncoding regions is much less abundant than data from coding regions. Since most published sequences are mRNAs, which do not include introns and flanking regions, the 5' and 3' untranslated regions are the only noncoding regions that can be studied in detail (Li, 1997). The present study represents an opportunity to study the molecular evolution of a noncoding region which is not transcribed and thus arguably has no function, unlike introns. This study is the first known to me which uses sequence data (rather than RFLPs, e.g. Jork & Kadereit, 1995; Yonemori *et al.*, 1996; Tebbitt, 1997) from this noncoding region to reconstruct phylogenetic relationships in higher plants.

3.1.4 COMBINED OR SEPARATE ANALYSIS

This subject has been dealt with by several authors from the perspective of whether to combine data sets i.e. "total evidence" (Kluge, 1989; Donoghue & Sanderson, 1992; Pennington, 1996), or compute a consensus of the separate analyses of the data sets (Mickevich & Farris, 1981; Miyamoto, 1985; Barrett *et al.*, 1991; 1993; Bull *et al.*, 1993; de Queiroz, 1993; Nelson, 1993), and the perspective of morphological versus molecular data (Donoghue & Sanderson, 1992; Givnish & Sytsma, 1997). Several authors have reviewed the options for combining data or producing consensus trees (Swofford, 1991; de Queiroz *et al.*, 1995; Miyamoto & Fitch, 1995; Huelsenbeck *et al.*, 1996; Page, 1996a). With the advent of multiple data sets for an increasing number of taxa, several authors have contemplated the options for combining these data sets

(Olmstead & Sweere, 1994; Hoot *et al.*, 1995; Mason-Gamer & Kellogg, 1996; Hoot *et al.*, 1997; Seelanan *et al.*, 1997). Despite much controversy and heated discussion, there appears to be a consensus of opinion now which is nicely summarised in the figure provided by Seelanan *et al.* (1997) (reproduced as fig. 3.1). I will discuss morphological versus molecular data in more detail in paragraph 3.4.5. Several assessments of character congruence were implemented. These are detailed in paragraph 3.2.5.

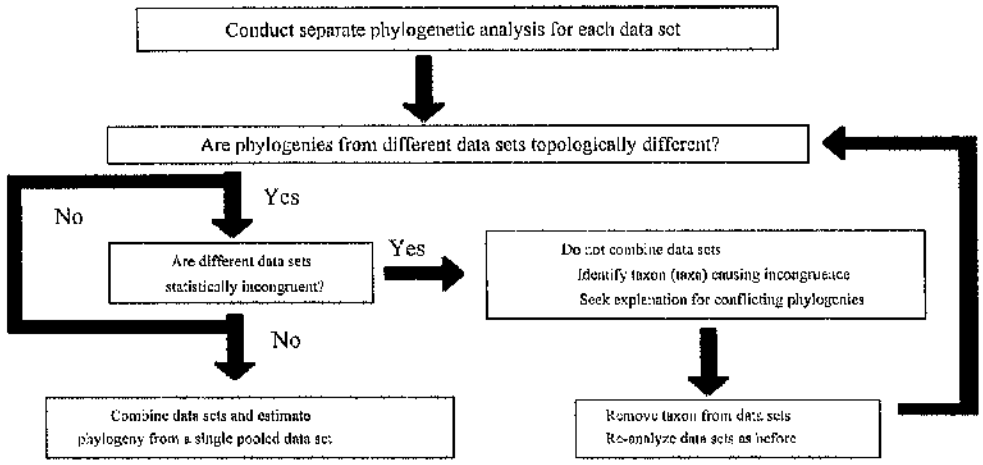


FIG. 3.1 SUGGESTED PROCEDURE FOR EVALUATING COMPETING TREES (SEELANAN *ET AL.*, 1997)

3.1.5 AIMS

The aims of this study are to (1) test the monophyly of section *Knesebeckia*; (2) produce a preliminary estimate of the phylogeny of *Begonia*; (3) investigate the characteristics of a noncoding region of chloroplast DNA; (4) compare the results of a phylogenetic analysis of mapped RFLP data with sequence data for the region *trn*C - *trn*D; (5) test the congruence of the phylogeny from the molecular data with that from the morphological data.

3.2 MATERIALS AND METHODS

Addresses for companies supplying chemicals and lab equipment are included in appendix F.

3.2.1 TAXA INCLUDED IN THE STUDY & CHOICE OF OUTGROUP

Datisca was chosen as the outgroup, based on cladistic analyses of *rbc*L sequence data (Chase *et al.*, 1993; Swensen *et al.*, 1994; Swensen, 1996; Swensen pers. comm., 1997; Badcock, unpublished analysis of sequence data in Genbank), 18S rDNA sequence data (Soltis *et al.*, 1997) and intuative opinions on morphology (Lindley, 1846; Lawrence, 1951; Dahlgren, 1980; Takhtajan, 1980; Cronquist, 1981; Thorne, 1992; Bouman & de Lange, 1983; Boeswinkel, 1984).

With no published phylogenetic framework in *Begonia*, it was necessary to sample the geographic and morphological variation of the genus, in order to test the monophyly of section *Knesebeckia*. As there are over 1000 species divided into c. 80 sections in *Begonia*, a pragmatic approach to sampling was taken. Taxa were included on the basis of unpublished molecular studies (Brouillet, pers. comm. and Swensen, pers. comm. both suggested that South American species should be included), published hypotheses relating to taxa in *Knesebeckia* (A. de Candolle, 1864; Irmscher, 1939; Burt-Utley, 1985; Jin & Wang, 1994), my personal observations of herbarium material in BM, E, K, L, MEXU, P and XAL and the availability of material for DNA extractions.

Seven *Knesebeckia* species from the American continent, including the type of the section and one Asian *Knesebeckia* species, *B. grandis* from China (the type of section *Diploclinium* - see paragraphs 2.1 & 4.2 for explanation) were included in this study. In total, 30 taxa were included in both the molecular and morphological analyses. Three taxa, *B.* cf. *grandis*, *B. dregei* accession 2 (acc. 2) and *B. ravenii* were included in an enlarged molecular analysis of 33 taxa. These taxa were not included in the morphological analysis as there was no point in including a multiple accession of *B. dregei* and there was a large amount of missing morphological data for the two other taxa.

All the taxa included in the molecular analysis are listed in table 3.1 with their distribution, current sectional placement, living collection accession number and source of material. The herbarium specimens examined for these taxa are listed in appendix A except for those from *B. grandis* which are listed in chapter 4.

TAXON	SECTION OF *BEGONIA*[1]	DISTRIBUTION[2]	ACCESSION NUMBER[3]	SOURCE[4]
B. acerifolia H.B.K	*Knesebeckia*	Ecuador	GL-001-057-96	F
B. acutifolia Jacq.	*Begonia*	West Indies	GL-002-147-66	F
B. convolvulacea (Klotzsch) A.DC.	*Enita*[5]	Brazil	GL-001-093-79	F
B. dipetala Graham	*Haagea*	S. India & Sri Lanka	GL-003-018-96	F
B. dregei Otto & Dietrich	*Augustia*	S. Africa	GL-004-026-94	F
B. floccifera Bedd.	*Reichenheimia*	S. India & Sri Lanka	GL-030-099-89	F
B. goegoensis N.E.Br.	*Reichenheimia*	Sumatra	GL-011-125-57	F
B. gracilis H.B.K.	*Knesebeckia*	Mexico	Z. Badcock 9	F
B. cf. *grandis* Dryand.*	*Knesebeckia*	Unknown	K-1977-8	S
B. grandis Dryand.	*Knesebeckia*	China	GL-004-085-80	F
B. heracleifolia Schltdl. & Cham.	*Gireoudia*	Mexico	GL-001-126-83	F
B. incarnata Link & Otto	*Knesebeckia*	Mexico	GL-011-089-95	F
B. malachosticta Sands	*Petermannia*	Malaysia: Sabah	GL-010-117-94	F
B. mannii Hook.f.	*Tetraphila*	W. Africa: Nigeria, Equatorial Guinea, Cameroon	GL-008-067-80	F
B. masoniana Irmsch.	*Coelocentrum*	? S. W. China, Indochina	GL-001-007-56	F
B. maynensis A.DC.	*Knesebeckia*	Peru, Ecuador	GL-001-107-92	F
B. meyeri-johannis Engl.	*Mezierea*	E. Africa: Zaire, Rwanda, Burundi, Uganda, Kenya, Tanzania	WAG-90PTKE017	S
B. oaxacana A.DC.	*Hexaptera*	Mexico & Central America	Z. Badcock 10	S
B. olbia Kerch.	*Knesebeckia*	Brazil	GL-002-117-94	F
B. aff. *palmata* D.Don	*Platycentrum*	Eastern Himalayas	GL-002-089-95	F
B. partita Irmsch. (=*B. dregei*)*	*Augustia*	South Africa	GL-002-036-89	F
B. peltata Otto & Dietrich	*Knesebeckia*	Mexico & Central America	GL-308-000-xx	F

TABLE 3.1 SUMMARY OF TAXA INCLUDED IN MOLECULAR CLADISTIC ANALYSIS

B. rajah Ridl.	*Reichenheimia*	Malaya	GL-003-081-96	F
B. ravenii C.I.Peng & Y.K.Chen*	*Diploclinium*	Taiwan	E-(ETE 24)-933938	F
B. roxburghii A.DC.	*Sphenanthera*[5]	N. E. India - Burma	Montreal-2331-54	F
B. rubella Buch.-Ham. ex D.Don	*Trilobaria*	Nepal	GL-005-094-94	F
B. salaziensis (Gaud.) Warb.	*Mezierea*	Réunion & Mauritius	K-1986-412	F
B. sutherlandii Hook.f.	*Rostrobegonia*	S. Africa & Tanzania	Ansells Garden Centre[6]	F
B. tayabensis Merr.	*Diploclinium*	Philippines	GL-006-035-89	F
B. ulmifolia Willd.	*Donaldia*	Venezuela	K-125-57	F
B. wollnyi Herzog	*Knesebeckia*	Brazil & Bolivia	GL-003-057-96	F
Datisca cannabina L.	Genus	S. W. Asia - Himalayas	E-19694093	F
Datisca glommerata (Presl) Baill.	Genus	California, U.S.A.	S. Swensen 767	?
Symbegonia sanguinea Warb.	Genus	New Guinea	GL-003 127-93	F

[1]According to Barkley & Golding (1974), with the exception of "Asian *Knesebeckia*" which were sometimes attributed to section *Begonia* (see paragraph 4.2 for a discussion of this nomenclature).

[2]Distributions according to Barkley & Golding (1974) except where additional information available in chapter 4, specimens cited in appendix A, Burt-Utley (1985), Klazenga *et al.* (1994), Sosef (1994) and de Wilde & Arends (1980).

[3] The letters preceding the accession numbers refer to the institution housing the accession; E = Royal Botanic Garden, Edinburgh, Inverleith Row, Edinburgh, EH3 5LR; GL = Glasgow Botanic Garden; K = Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB; Montreal = Jardin botanique, 4101, rue Sherbrooke Est., Montréal, Québec, H1X 2B2, Canada; WAG = Wageningen Agricultural University, P.O.B. 8010 6700 ED Wageningen, The Netherlands.

[4] Abbreviations for source are: Fresh / frozen leaves; Silica gel dried leaves.

[5] Placed in new (but unpublished) section *Dioecibegonia* M.T.Tebbitt (1997).

[6] Ansells Garden Centre, High Street, Horningsea, Cambs., England; courtesy of Dr. Mark Tebbitt, Brooklyn Botanic Garden, New York, U.S.A.

* These taxa were not included in the morphological and combined analyses.

TABLE 3.1 CONTD.

3.2.2 MORPHOLOGICAL DATA

The 66 morphological characters included here are the result of a preliminary morphological investigation of *Begonia*, as presented in chapter 2. The data was compiled from herbarium material (see appendix A) and the monographs of Burt-Utley (1985), Klazenga *et al.* (1994), Sosef (1994) and de Wilde & Arends (1980). The morphological characters and states used in this analysis are given in table 2.1, chapter 2, and are discussed in paragraphs 2.2.2.1-2.2.2.5. The morphological data set is a subset of that illustrated in table 2.3. The amount of missing data is 5.9%, 54 characters are parsimony informative [*sensu* PAUP* (Swofford, in prep)] and 4 characters are constant.

3.2.3 MOLECULAR DATA

Tebbitt (1997) reported that the *trn*C - *trn*D region in *Begonia* is about 3 Kb in length, although demonstrating length variation of up to c. 1 Kb between some species. During the present study it was not possible to sequence the entire region due to time constraints. Using the universal primers anchored in the tRNA genes, I sequenced into the intergenic region from both ends and then used internal primers to extend the sequence towards the centre of the region. This approach is summarised in fig. 3.2. Although double strand sequencing was not carried out the internal primers were located so that there was approximately a 50% overlap in the sequence generated on one strand.

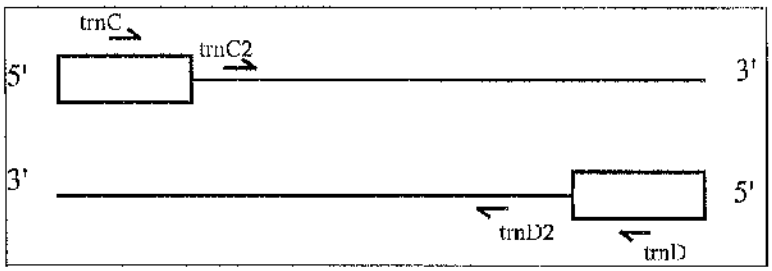


FIG. 3.2 APPROACH FOR SEQUENCING THE *TRN*C - *TRN*D INTERGENIC CHLOROPLAST REGION

3.2.3.1 COLLECTION OF MATERIAL

All plant material from Glasgow and Edinburgh was collected into, and stored in, liquid nitrogen until the DNA was extracted. Material from the Royal Botanic Gardens, Kew, Wageningen Agricultural University and field collections in Mexico was collected in silica gel (after Chase & Hills, 1991). *B. gracilis* was collected as a tuber in Mexico and grown up in Glasgow Botanic garden. The accession from Dr. S. M. Swensen was donated as a suballiquot of DNA.

3.2.3.2 DNA EXTRACTION

DNA extractions were carried out using either the CTAB extraction method described by Doyle & Doyle (1987) with 1% PVP (polyvinylpolypyrrolidone) added to the extraction buffer (see appendix G) or a version of this extraction procedure scaled down to microfuge tubes (P. Hollingsworth, pers. comm.) (see appendix H).

3.2.3.3 PCR CONDITIONS ETC.

The primers used were those published by Demesure *et al.* (1995) (supplied by Bioline (UK) Ltd.). The DNA sequence of these primers is listed in table 3.2, together with the internal primers designed in this study (see paragraph 3.2.3.5). The template for PCR amplification consisted of c. 50-100 ng of genomic DNA. The reaction mixture (50 µl) contained 67 mM Tris-HCl, 2 mM $MgCl_2$, 16 mM $(NH_4)_2SO_4$, 0.01% Tween-20 in the reaction buffer, 2.5 mM of each of the four dNTPs (Pharmacia Biotech Ltd.), 0.05 µM of each primer and 0.5 units of *Taq* polymerase (Bioline (UK) Ltd.) (The PCR recipe is summarised in appendix B). The amplification was carried out using 1 cycle of 4 min at 94°C, 35 cycles of 45 sec at 92°C, 45 sec at 58°C, 2 min at 72°C and 1 cycle of 10 min at 72°C on a Perkin Elmer 480 thermal cycler. The PCR products were visualised by UV fluorescence after electrophoresis on agarose gel (1-1.6%) and stained with ethidium bromide (0.2 µg / ml).

The amplified DNA samples were purified using Promega Wizard PCR preps DNA Purification System or QIAGEN QIAquick clean ups; the latter method was found to be more reliable and easier to use. The protocols for these procedures are included in appendix E.

3.2.3.4 SEQUENCING PROTOCOL

The purified amplified DNA samples were sequenced using the standard cycle sequencing 20 µl reactions following the manufacturer's recommendations (Applied Biosystems). These protocols are summarised in appendices D and E. Primers used for sequencing were "*trn*C", "*trn*D", "Beg-*trn*C2-F", "Beg-*trn*D2-F", "Dat-*trn*C2-F", "Dat-*trn*D2-F", "Dat-*trn*C-B" and "Dat-*trn*D-B"(see table 3.2). Sequences were obtained using a Perkin Elmer Applied Biosystems 373 automated fluorescent DNA Stretch Sequencer using the service provided by the Molecular Biology Support Service, Glasgow University. For base calling, proof-reading and editing I used Apple Macintosh computers with Applied Biosystems software (Sequence Navigator 1.0.1).

Although the universal primers of Demesure *et al.* amplified the *trn*C-*trn*D region of *Datisca cannabina* and *D. glommerata*, when these primers were used for sequencing these species the sequence was quite degenerate and only short pieces of sequence were readable. From these short sequences I was able to design primers specific for *Datisca* (Dat-*trn*C2-F, Dat-*trn*C-B, Dat-*trn*D2-F, Dat-*trn*D-B) (see table 3.2 for sequence details) and these were then used in the cycle sequencing reactions. The length of sequence generated by this method that was comparable with *Begonia* was still quite short and as the combined sequence of *D. cannabina* and *D. glommerata* was longer, I used a consensus of the two sequences to root the analysis of *Begonia*. When the sequences of *D. cannabina* and *D. glommerata* were different to each other, the consensus sequence was scored as missing (?).

The priming sites for the internal primers were absent in some of the *Begonia* species due to deletion events. In these cases the amount of comparable nucleotide sites was

only sometimes less than in those cases where internal primers were used, depending upon the length of the deletion.

3.2.3.5 INTERNAL PRIMER DESIGN

The programme *Primer3* (Rozen & Skaletsky, 1996) was used to help design the internal primers used in this study. This programme is used interactively via the internet and is available at the following location:

http://www-genome.wi.mit.edu/genome_software/other/primer3.html

Few references were found that aided in the design of primers and I have therefore included a summary of helpful information (see appendix J).

CODE NAME OF PRIMER	DNA SEQUENCE*
*trn*C (Demesure *et al.*, 1995)	5'-CCAGTTCAAATCTGGGTGTC-3'
*trn*D (Demesure *et al.*, 1995)	5'-GGGATTGTAGTTCAATTGGT-3'
BEG-*TRN*C2-F	5'-GGAATCATTAAATCTTGATA-3'
BEG-*TRN*D2-F	5'-TGGTAGAATCATATTCAGGATTCA-3'
BEG-*TRN*D3-F	5'-CTAAGATCAAACAAGGATTCCA-3'
BEG-*TRN*C3-F	5'-ACTCTGCACTAGTGATTTCAC-3'
BEG-*TRN*C1-R	5'-AACCAGTCAGCAGCCACTAC-3'
BEG-*TRN*D1-R	5'-TGGAATTTTTGTATGTGCTC-3'
DAT-*TRN*C-B	5'-AGTATCTTCCGCCCTTTCTG-3'
DAT-*TRN*D-B	5'-TGGTATCCCTTGGAATCCTG-3'
DAT-*TRN*C2-F	5'-CATGAAAGTTTCTGAGTGCTCC-3'
DAT-*TRN*D2-F	5'-CAAGGGATACCATACCGGGTC-3'

* The location of these primers is indicated in the molecular data set (appendix K).

TABLE 3.2 DNA SEQUENCE OF PRIMERS USED IN THIS STUDY AND THOSE DESIGNED FOR FUTURE USE WITHIN THE CPDNA REGION *TRN*C-*TRN*D

3.2.3.6 SEQUENCE ALIGNMENT

Initial sequence alignment was done by aligning pairs of sequences with the comparative alignment command in Sequence Navigator version 1.0.1 (Applied Biosystems, Inc.). The clustal multiple alignment option was not useful due to the large number of indels and their large range in size. Sequences were then pasted into the programme Se-Al v.1.d1 (Rambaut, 1995) and aligned by eye to minimise gaps.

There are 2450 *trn*C - *trn*D 'nucleotide positions' in this data set with the actual number of bases ranging from 835 in *B. salaziensis* to 1621 in *B. rubella*. The nucleotide

positions 777-901, 1138-1239, 1330-1332, 1424-1436 and 2359-2450, totalling 335 sites, were excluded from all analyses as they included a lot of missing data. Large amounts of missing data can lead to branch-swapping eddies during phylogenetic analysis (Novacek, 1992) and this can increase the analysis time greatly (pers. ob.). This is a result of dramatic increases in the number of possible trees with increasing amounts of missing data. From the remaining 2115 nucleotide sites 179 are parsimony informative [*sensu* PAUP* (Swofford, in prep)] and 1541 characters are constant. With the addition of 111 binary indel characters (chars. 2451-2562; see below) of which 26 are parsimony informative [*sensu* PAUP* (Swofford, in prep)] and 3 characters are constant, a total of 2226 characters was included in my *trn*C - *trn*D analyses. The amount of uncertainty in the sequence data is 0.95% if gaps are not considered, and 20.9% in the indel data.

3.2.4 PHYLOGENETIC ANALYSES

Parsimony analyses were conducted using PAUP* 4.0d60 (Swofford, in prep). All characters (2226 molecular and 66 morphological) were unordered and weighted equally, in the separate as well as in the combined analyses. The morphological data were treated as in chapter 2. In the molecular data set, gaps were coded with hyphens (-) and treated as missing in the PAUP* analyses. All the gaps were scored as present (0), absent (1) or missing (?) when not applicable (e.g. due to the presence of a large indel). Gaps associated with length varation in SSRs were not scored. This yielded 111 additional binary characters. This insertion - deletion (indels) data set is displayed in appendix M. All the gaps, rather than just informative gaps (as in Eriksson & Donoghue, 1997) were scored so that the branch lengths would reflect the amount of change more accurately.

In order to see the effect of each data set the following analyses were conducted: sequence data only [33 taxa]; indels binary data only [33 taxa]; sequence and indels data

combined [33 and 30 taxa]; morphological data only [30 taxa]; sequence, indels and morphological data combined [30 taxa].

Heuristic searches were conducted with MULPARS (retention of all equally parsimonious trees), STEEPEST DESCENT (does not abandon a round of swapping until all input trees from the previous round have been examined by the swapping algorithm) [not in morphology search] and TBR (Tree-Bisection-Reconnection) branch swapping, in effect [this is the most complete searching algorithm without using branch and bound or exhaustive searches]. Starting trees were constructed using 100 replicates of random addition sequences for the molecular and combined data sets, and 10 replicates for the morphological data set in order to contain the search time. The use of replicates of random addition sequence facilitates the search for islands of equally most parsimonious trees (Maddison, 1991). To assess node support, bootstrap analyses (Felsenstein 1985; Hillis & Bull 1993; Sanderson, 1995) were performed, as were decay analyses (Bremer, 1988; 1994; Donoghue *et al.*, 1992) using the reverse constraint option in PAUP* and the AutoDecay program of T. Eriksson (1997). In the bootstrap runs, PAUP* was set to run 100 bootstrap replicates with NNI (Nearest-Neighbour-Interchange) branch swapping. In the reverse constraint runs for the decay analyses PAUP* was set to run 10 random addition sequences. Alternative phylogenetic arrangements and the evolution of particular morphological characters were tested using Maclade 3.05 (Maddison & Maddison 1992). Consistency and retention index values were obtained from PAUP*.

3.2.5 COMPARING RFLP DATA AND SEQUENCE DATA FROM THE *TRNC* - *TRND* REGION

As explained in paragraphs 3.1.2 and 3.2.3, Tebbitt (1997) investigated the variation present in the *trn*C - *trn*D region using PCR-RFLPs. This study produced 16 binary characters for 14 taxa comparable with those used in the present study and these are reproduced in appendix L. Two taxa, *B. chlorosticta* and *B. hatacoa*, have been included

from Tebbitt's study which were not sequenced by me but are intended to be compared with *B. malachosticta* and *B.* aff. *palmata* respectively due to their very similar morphologies.

A reduced data set of my molecular data (sequence + indels) was analysed to compare with an analysis of RFLP data. Branch and bound searches were conducted with the MULPARS setting in effect, starting from a simple addition sequence. The congruence of the data sets was examined as in paragraph 3.2.6.

3.2.6 CONGRUENCE OF DATA SETS

Before combining the data sets, several methods of assessing congruence among the data sets were implemented: visual comparison of the various clades found in the strict consensus of the trees, their bootstrap support, and calculation of incongruence indices I_{MF} and I_M. To assess the statistical significance of I_{MF}, the partition homogeneity test was used (Farris *et al.*, 1995; implemented with PAUP* 4.0d60).

The Mickevich and Farris incongruence index (I_{MF}) is the proportion of the total incongruence due to between-data-set incongruence (calculated by using the number of extra steps on minimal individual and combined trees: Mickevich & Farris, 1981; Swofford, 1991; Johnson & Soltis, in press). Like I_{MF}, the Miyamoto incongruence index (I_M) also partitions the total incongruence into between- and within-data set components (described in Kluge, 1989; Swofford, 1991; Johnson & Soltis, in press). However, rather than combining the two data sets, each data set is mapped onto the minimal tree computed for the other data set. Both I_{MF} and I_M can range from zero (perfect agreement between data sets) to one (no agreement between data sets). When multiple shortest trees were obtained in this study, I_M values were computed using the shortest tree length found when trees from one data set were superimposed on another data set.

Whereas I_{MF} and I_M provide a quantitative measure of incongruence, they do not provide a statistical basis for evaluating incongruency. The partition-homogeneity test randomly partitions characters (Farris *et al.*, 1995; implemented with PAUP* 4.0d60). It tests the null hypothesis that a given partition of a data set represents a random partition of the data. If two data sets are highly incongruent, then the sum of their minimal trees should be significantly shorter than that of the sum of the tree lengths from random partitions of the combined data and the null hypothesis will be rejected. The data sets were analysed with 100 replicates, the heuristic search option with simple addition sequence, NNI and MULPARS in effect; max trees were set to 1000 with no prompt for their increase.

3.3 RESULTS

The results are presented in four sections: morphology, molecular, combined and RFLP vs. sequence. The morphological data set is only presented briefly as it has been discussed in detail in chapter 2. The analysis of the molecular data set is discussed in relation to the composition of the sequence data, the phylogenetic input of the substitution and indel data and the relationships suggested by the data. The decision as to whether to combine the data is discussed and the resulting relationships compared with the molecular data set alone. Finally the RFLP data generated by Tebbitt (1997) is re-analysed here and compared to an analysis of the sequence data generated here.

3.3.1 ANALYSIS OF MORPHOLOGICAL DATA SET

The phylogenetic analysis of the morphological data set of 66 characters for 30 taxa resulted in 19 trees of 286 steps (CI = 0.3566, RI = 0.4682). These trees were distributed in 3 islands of equally parsimonious trees (*sensu* Hendy *et al.*, 1988; Maddison, 1991). The tree island profile is illustrated in table 3.3. A strict consensus of all 19 trees is presented in fig. 1 This consensus represents the most conservative estimate of the phylogenetic relationships of these taxa based on this morphological data set.

As one might expect from a large analysis of morphology, few clades are well supported; only two clades, *B. gracilis-B. grandis* and *B. malachosticta-Symbegonia sanguinea* are supported by bootstrap values greater than 50%. The most significant outcome of this analysis is that *B. grandis* and *B. gracilis*, two *Knesebeckia* from Asia and Mexico respectively, occur as a monophyletic clade supported by a bootstrap of 66% and a Bremer support value of 3; however, the remaining *Knesebeckia* are unresolved at the base of the tree. When these data were analysed in a more comprehensively sampled study (see chapter 2) they did not form a monophyletic group and, in forcing *Knesebeckia* to be monophyletic, the tree had to be 8 steps longer. This would therefore indicate that sampling may well have a considerable effect on the outcome of this phylogenetic analysis; Lecointre *et al.* (1993) proposed that sampling could be very important in the outcome of molecular systematic studies.

Island	Size	First tree	Last tree	Score	First replicate	Times hit
1	2	1	2	286	1	2
2	3	3	5	286	3	3
3	14	6	19	286	5	2
4	2			287	8	1
5	10			288	2	1
6	4			288	4	1

TABLE 3.3 TREE ISLAND PROFILE OF MORPHOLOGICAL DATA SET FOR 30 TAXA

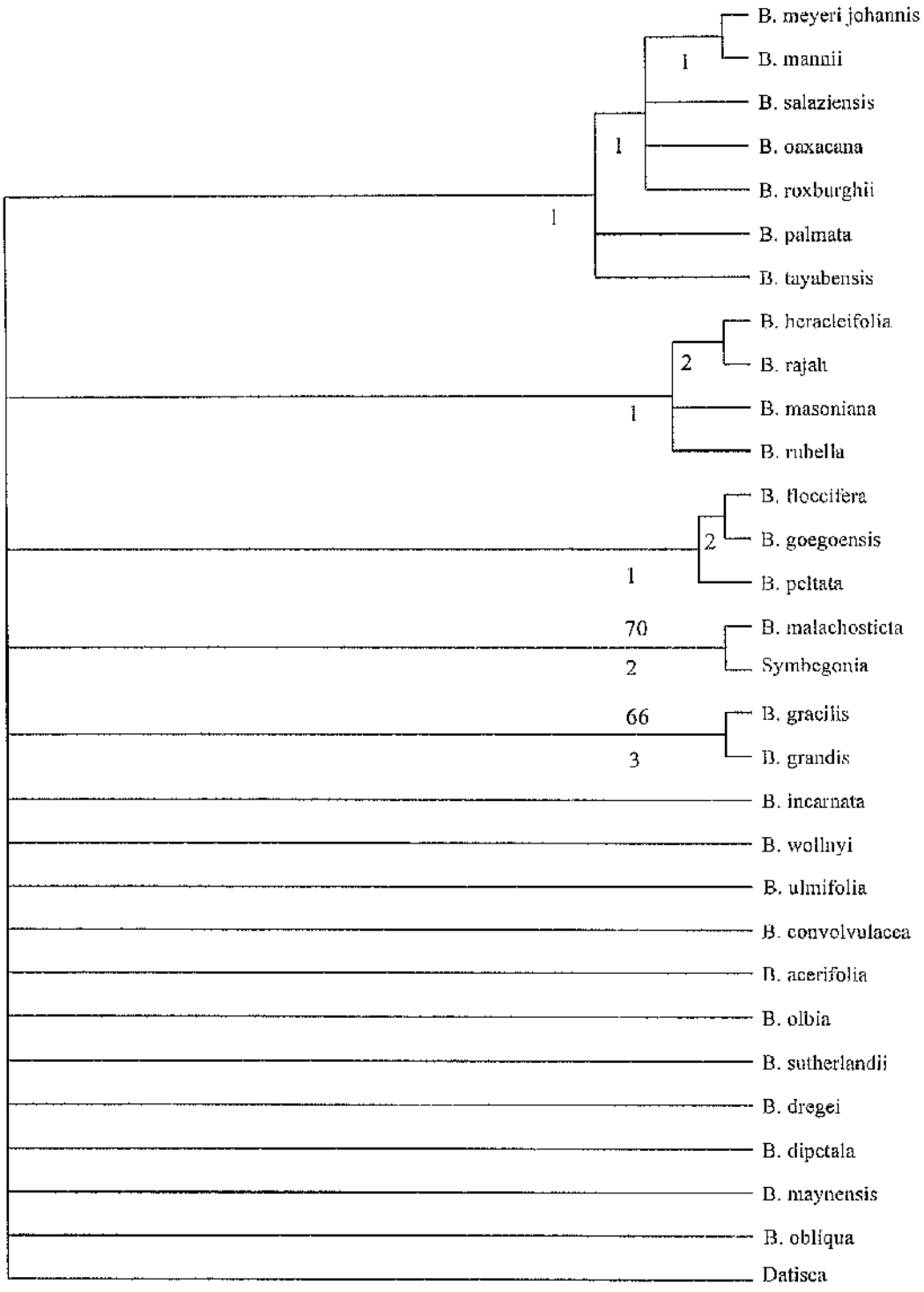


FIG. 3.3 STRICT CONSENSUS TREE OF 19 EQUALLY MOST PARSIMONIOUS TREES OF 286 STEPS (CI = 0.3566, RI = 0.4682) PRODUCED FROM THE CLADISTIC ANALYSIS OF THE MORPHOLOGICAL DATA SET. NUMBERS ABOVE THE LINES INDICATE BOOTSTRAP SUPPORT GREATER THAN 50%; NUMBERS BELOW THE LINES INDICATE BREMER SUPPORT VALUES.

3.3.2 ANALYSIS OF MOLECULAR DATA SET

3.3.2.1 CHARACTERISATION OF THE *TRN*C - *TRN*D NONCODING CPDNA REGION

In this study the *trn*C - *trn*D region was found to vary in length from c. 3000 - 4000 bases. One interesting observation of this variation in length is that species occurring at the base of the molecular phylogeny of *Begonia* appear to have the greatest amount of DNA in this region, suggesting a possible evolutionary trend towards a decrease in the size of this intergenic region.

The mean base composition of the sampled *trn*C - *trn*D region is presented in table 3.4. The region is appreciably AT rich. Another feature of this noncoding region is the large number of Simple Sequence Repeat regions (SSRs) which account for c. 9% of the sequence generated.

A	C	G	T
0.3389	0.13957	0.15714	0.36439

TABLE 3.4 MEAN BASE COMPOSITION OF *TRN*C - *TRN*D SEQUENCE

Sequence divergences (calculated using PAUP* command "calculate pairwise distances") within *Begonia* range from 1-9%, whereas between *Begonia* and *Datisca* species they range from 16-24%, estimated using the HKY85 model (Hasegawa-Kishino-Yano 1985 model, Hasegawa *et al.*, 1985). This model allows unequal equilibrium base frequencies (see paragraph 3.3.2.1) and takes into account the common observation that transitions and transversions occur at different rates (Swofford *et al.*, 1996). It should be noted that this form of sequence divergence estimate accounts only for the rate of substitutions and does not take account of insertion and deletion (indel) events. Indel events are a common feature of noncoding regions (Li & Graur, 1991; Li, 1997) and tend to occur at approximately the same rate as substitutions in noncoding

regions (Curtis & Clegg, 1984; Wolfe *et al.*, 1987; Zurawski & Clegg, 1987; Clegg *et al.*, 1991; Clegg & Zurawski, 1992; Gielly & Taberlet, 1994b).

3.3.2.2 COMPARISON OF PHYLOGENETIC SIGNAL OF SUBSTITUTIONS AND INDELS

The strict consensus trees of the separate analyses of the substitution and indel data sets are largely complementary. Both data sets have high consistency and retention indices, although those of the indel data set are slightly higher indicating less conflict in the data set. In general, the substitution data set gives greater resolution within clades. The significant differences between the two trees are the position of the clade including *B. olbia* and the resolution of a clade including *B. masoniana* in the indel data set. When the indels are analysed separately they place the *B. olbia* clade within a clade containing the Central American, South and East African *Begonia* and the Indian *B. floccifera*, while in the analysis of the sequence (substitutions only) data, the *B. olbia* clade is placed as sister to all *Begonia* except the fleshy fruited African species. The substitution data do not resolve the position of *B. masoniana*, *B. malachosticta* and *Symbegonia sanguinea* relative to most of the included *Begonia* but the indels indicate that these three taxa are included in a clade with other Malesianan *Begonia* (see fig. 3.5).

	Tree Length	CI	RI	No. of Trees
33 Taxa				
Sequence only	846	0.8109	0.6863	304
Indels only*	126	0.8730	0.8161	35 692
Sequence + indels	975	0.8164	0.7002	8
30 Taxa				
Sequence + indels	955	0.8222	0.6724	8
Morphology only	286	0.3566	0.4682	19
Combined	1302	0.6813	0.5202	4
14 Taxa				
RFLP	26	0.615	0.756	12
Sequence + indels	393	0.908	0.687	2

* Analysis stopped when tree buffer overflowed

TABLE 3.5 COMPARISON OF TREE STATISTICS FOR THE DIFFERENT ANALYSES

3.3.2.3 PHYLOGENETIC RELATIONSHIPS BASED ON THE MOLECULAR DATA SET

When all the molecular data (substitutions and indels) are analysed together the result is eight equally most parsimonious trees of 975 steps. This is only 3 steps longer than the combined separate analyses. The combined molecular analysis of 33 and 30 taxa are illustrated in fig.s 3.6 and 3.7 respectively. There are strong bootstrap and Bremer support values for the majority of resolved nodes. *B. meyeri-johannis* (sect. *Mezierea*), *B. salaziensis* (sect. *Mezierea*) and *B. mannii* (sect. *Tetraphila*) form the basal dichotomy with the rest of *Begonia*. The remaining clades, containing more than one taxa, are all well defined geographically, as indicated on fig. 3.6. Perhaps the most interesting geographical relationship is between South Africa and Central America, with *B. sutherlandii* and *B. dregei* occurring as sister to species from sections *Begonia*, *Gireoudia* and *Knesebeckia*.

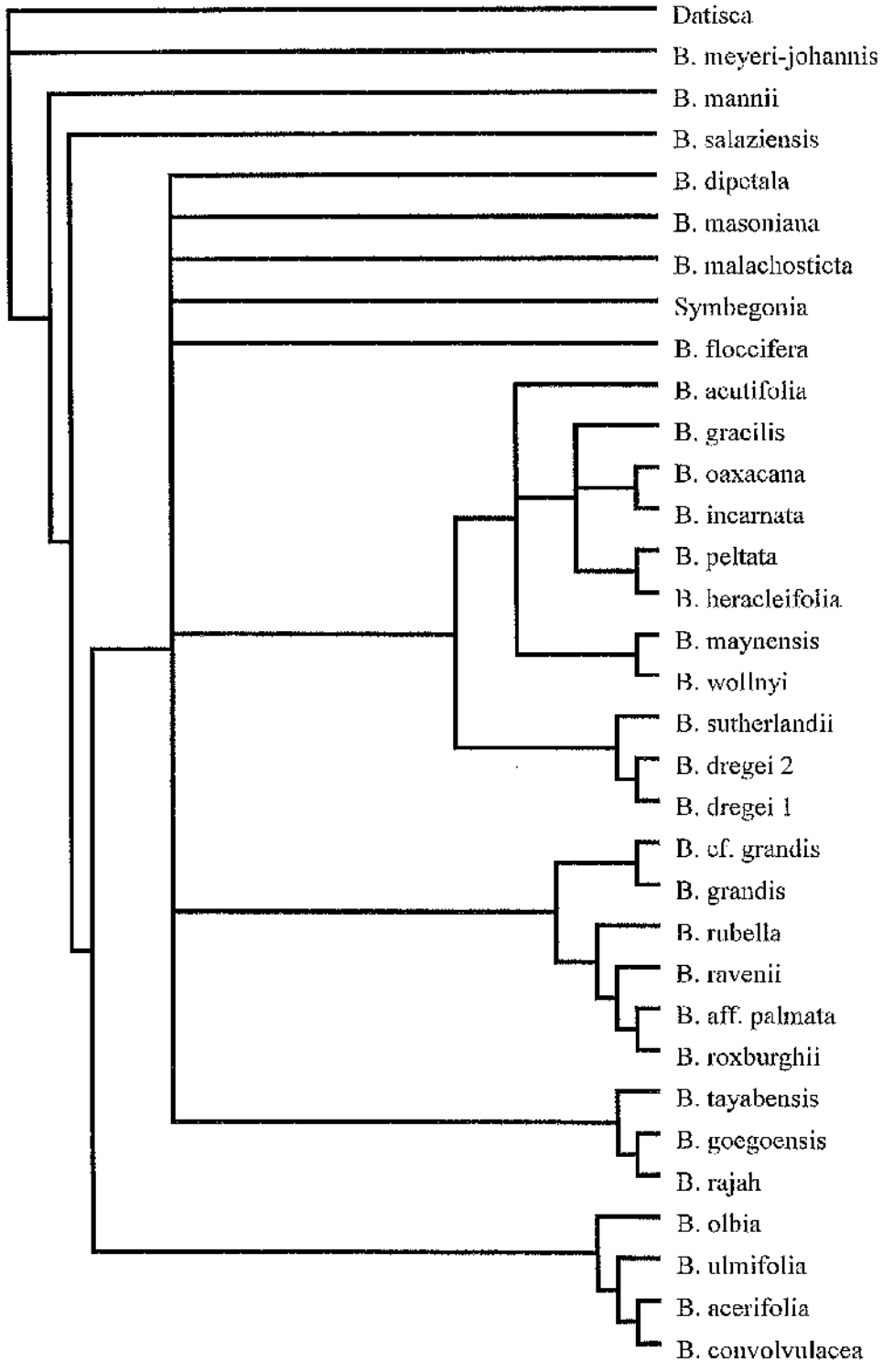


FIG. 3.4 STRICT CONSENSUS OF 304 EQUALLY MOST PARSIMONIOUS TREES OF 846 STEPS (CI = 0.8109, RI = 0.6863) PRODUCED FROM THE CLADISTIC ANALYSIS OF *TRN*C - *TRN*D SEQUENCE DATA (SUBSTITUTIONS ONLY).

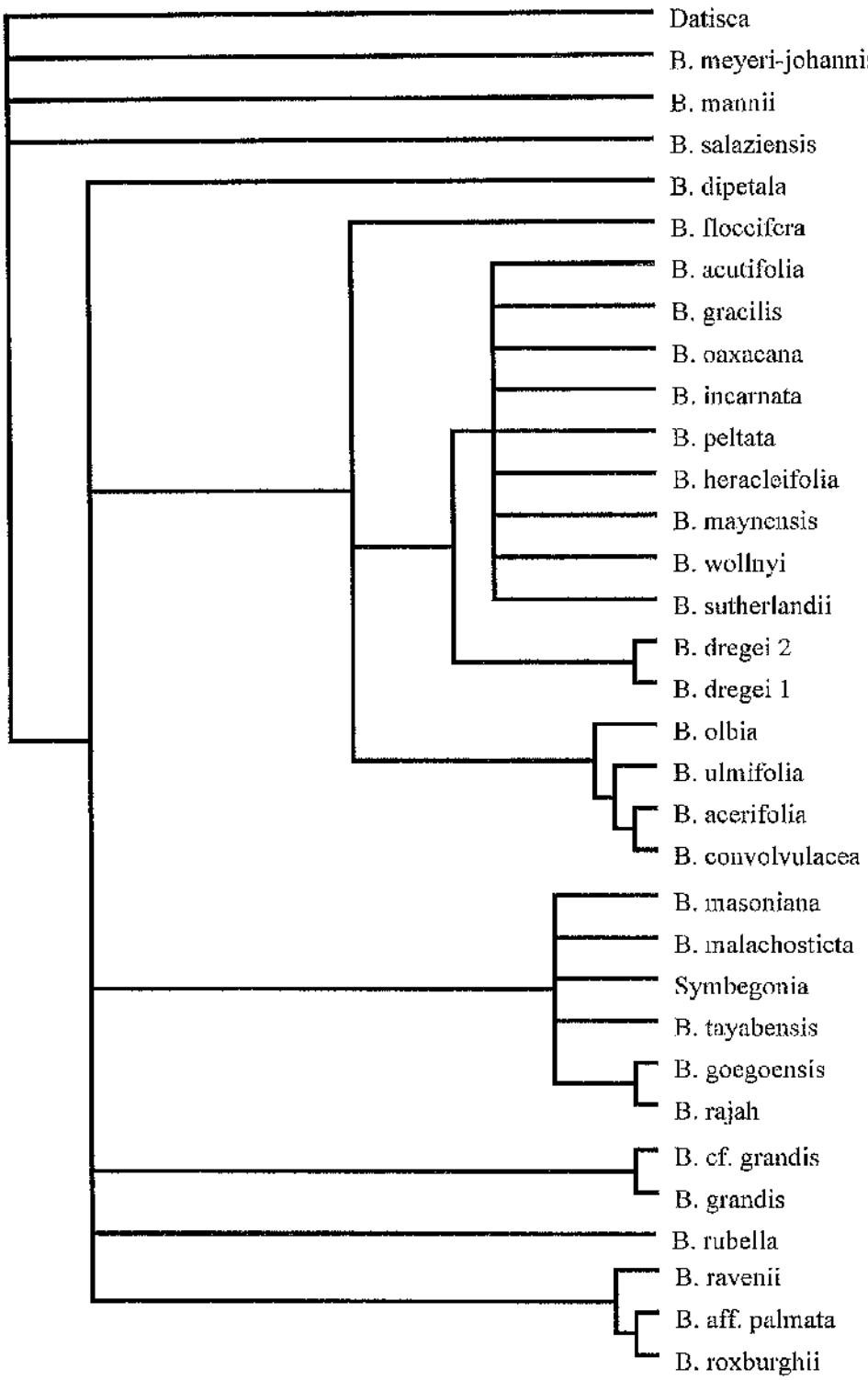


FIG. 3.5 STRICT CONSENSUS OF 35692 EQUALLY MOST PARSIMONIOUS TREES OF 126 STEPS (CI = 0.8730, RI = 0.8161) PRODUCED FROM THE CLADISTIC ANALYSIS OF *TRNC - TRND* SEQUENCE DATA (INDELS ONLY).

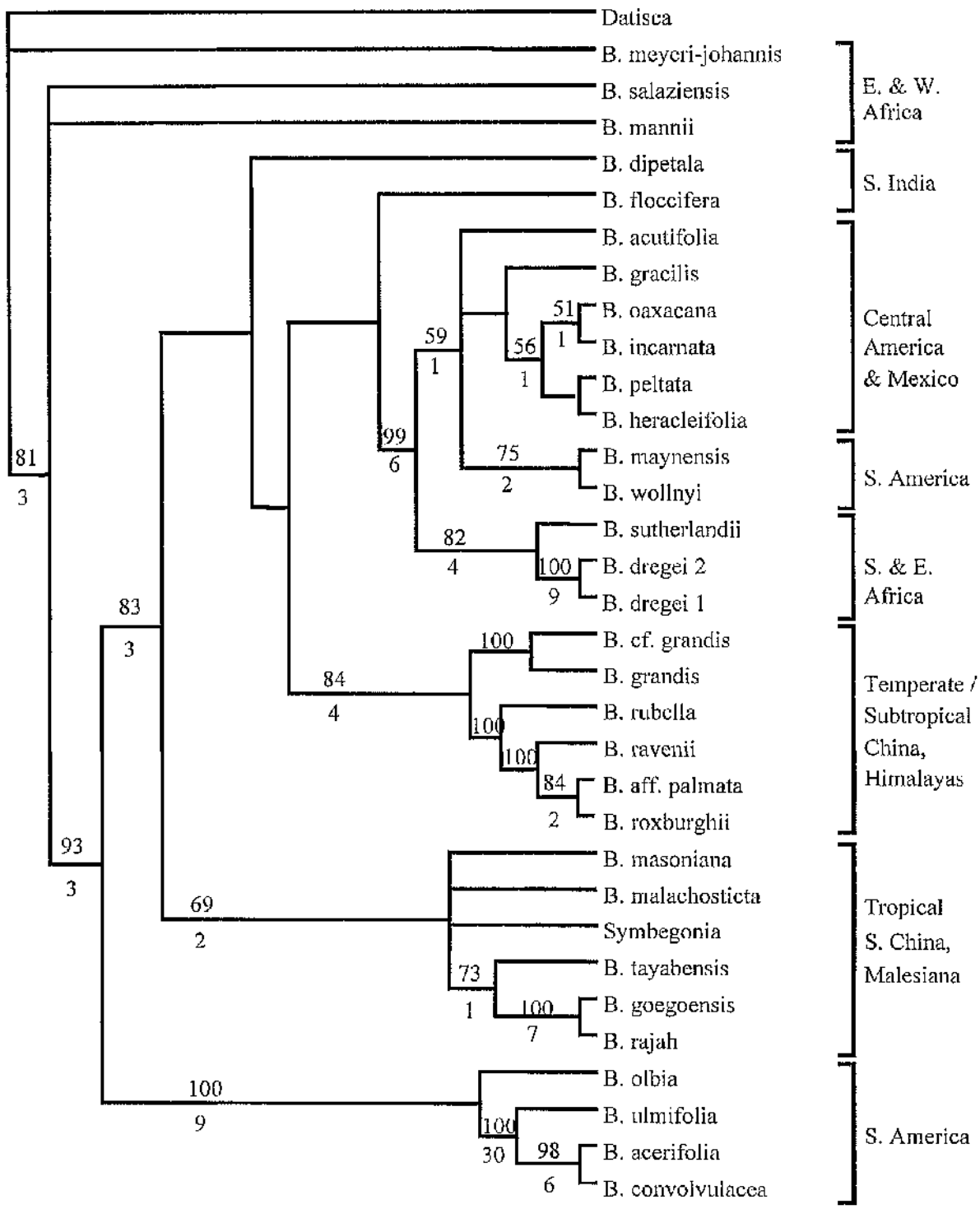


FIG. 3.6 STRICT CONSENSUS OF 8 EQUALLY MOST PARSIMONIOUS TREES OF 975 STEPS (CI = 0.8164, RI = 0.7002) PRODUCED FROM THE CLADISTIC ANALYSIS OF *TRN*C - *TRN*D SEQUENCE DATA (SUBSTITUTIONS AND INDELS) FOR 33 TAXA. NUMBERS ABOVE BRANCHES INDICATE BOOTSTRAP SUPPORT GREATER THAN 50% AND NUMBERS BELOW LINES INDICATE BREMER SUPPORT VALUES.

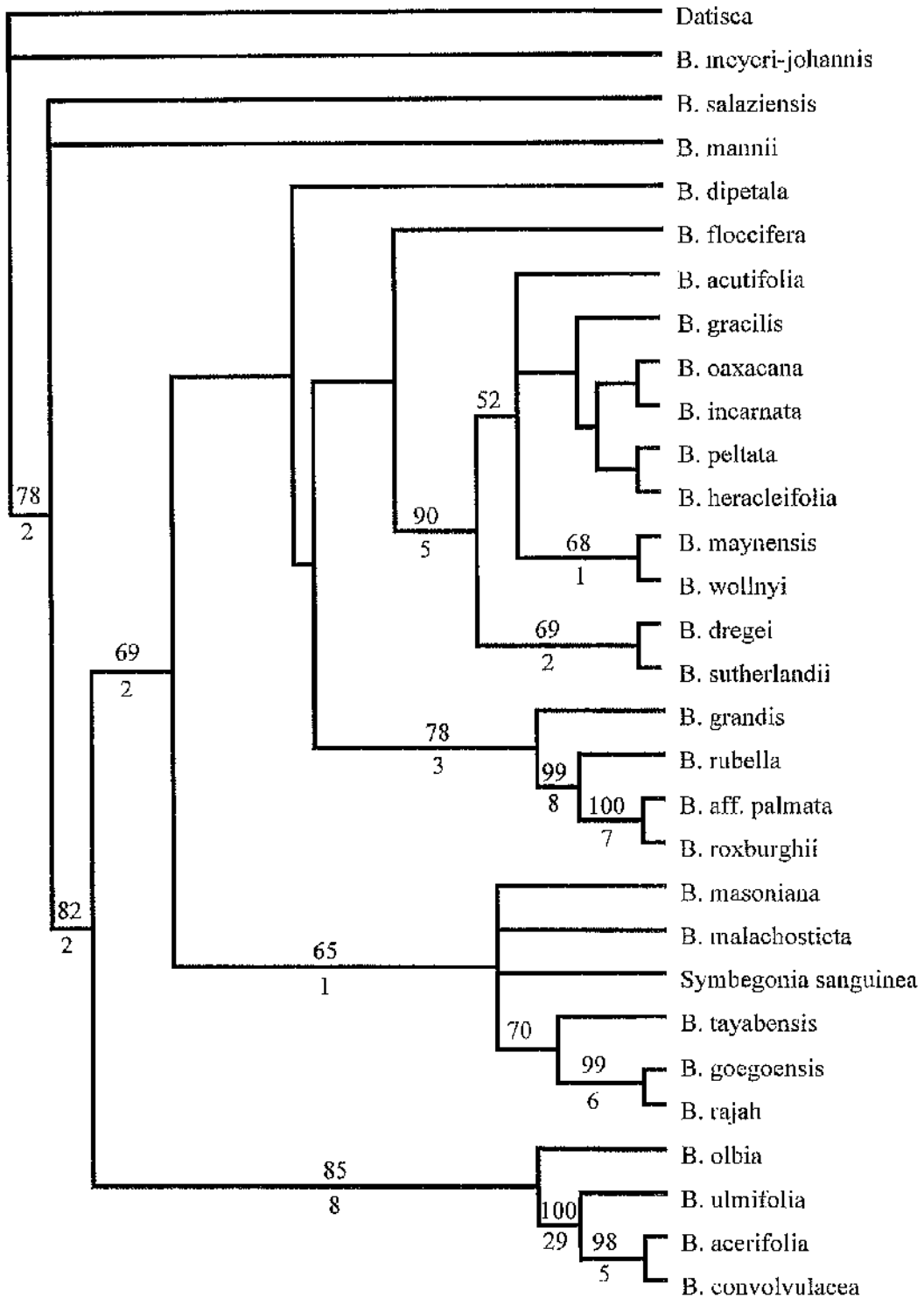
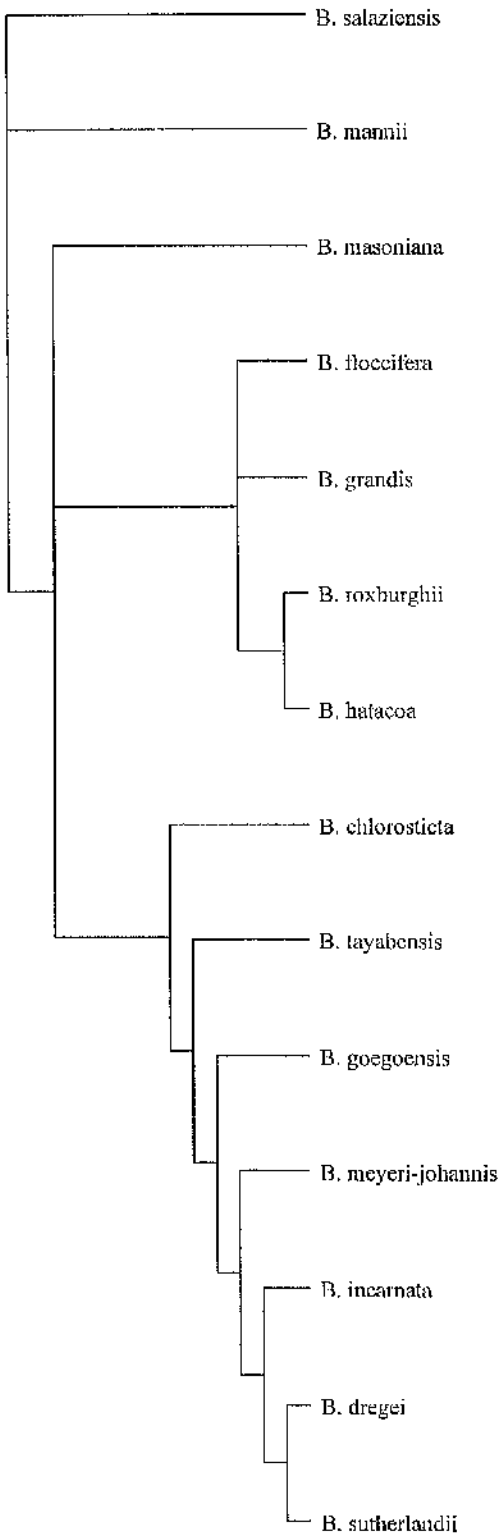


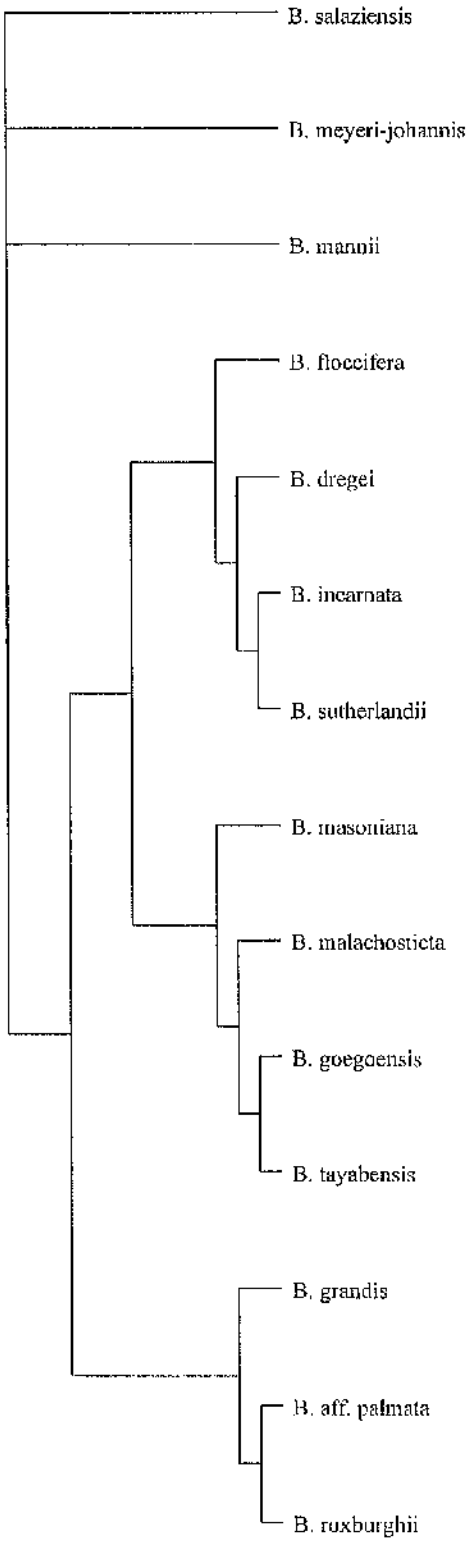
FIG. 3.7 STRICT CONSENSUS OF 8 EQUALLY MOST PARSIMONIOUS TREES OF 955 STEPS (CI = 0.8222, RI = 0.6724) PRODUCED FROM THE CLADISTIC ANALYSIS OF *TRNC - TRND* SEQUENCE DATA (SUBSTITUTIONS AND INDELS) FOR THE REDUCED DATA SET OF 30 TAXA. NUMBERS ABOVE BRANCHES INDICATE BOOTSTRAP SUPPORT GREATER THAN 50%, NUMBERS BELOW BRANCHES INDICATE BREMER SUPPORT VALUES ≥ 1.

3.3.3 COMPARING THE SEQUENCE AND RFLP DATA

The branch and bound search of the RFLP data resulted in 12 equally most parsimonious trees of 26 steps. The trees were rooted using *B. salaziensis*. Two characters are parsimony-uninformative. Figure 3.8 shows the 50% majority rule trees for the RFLP and sequence data. Two taxa have different positions in these analyses; in the RFLP analysis *B. meyeri-johannis* does not group with the other African fleshy fruited species (*B. mannii* and *B. salaziensis*) but as the sister taxon to a clade containing *B. incarnata*, *B. dregei* and *B. sutherlandii* while *B. floccifera* is the sister taxon to *B. roxburghii* and *B. hatacoa* rather than sister taxon to the *dregei-sutherlandii-incarnata* clade in the sequence analysis. Along with these major differences, the RFLP and sequence data differ in the branching order of the *dregei-sutherlandii-incarnata* clade and the occurrence of a dichotomy between the *dregei-sutherlandii-incarnata-floccifera* clade and the *masoniana-malachosticta-goegoensis-tayabensis* clade in the sequence data but not in the RFLP data. The results of the tests of incongruence are presented in table 3.6. When the RFLP data was mapped onto the trees derived from the sequence and indel data, the data required nine more steps to fit the tree.



RFLP Data (Consensus of 12 trees; TL = 26; CI = 0.615; RI = 0.756).



Sequence Data (Consensus of 2 trees; TL = 393; CI = 0.908; RI = 0.687).

FIG. 3.8 50% MAJORITY RULE CONSENSUS TREES OF 14 TAXA ANALYSED FOR A RFLP AND A SEQUENCE DATA SET FROM THE CPDNA REGION *TRN*C - *TRN*D.

3.3.4 COMBINING THE DATA SETS

The results of the tests of incongruence presented in table 3.6 indicate that the morphological and molecular data sets are significantly incongruent, implying that these two data sets should not be combined. On the basis of bootstrap, Bremer support, consistency and retention indices, the molecular data is much better supported (and therefore "better"?) than the morphological data set. These results would therefore suggest that more confidence can be placed in the molecular data set.

I proceeded to investigate the result of combining the two data sets despite this result in order to test the effect of "total evidence". The resulting tree requires 61 steps more than the combined lengths of the separate analyses of these data sets and is illustrated in fig. 3.9. One of the four equally most parsimonious trees resulting from the combined data is shown in fig. 3.10. There are several differences in the strict consensus of this combined data set and that of the molecular data set (the data set which would be expected to contribute more to the combined analysis due to the number of parsimony informative characters, the CI, RI and the branch support as indicated by the bootstrap and Bremer support values). Firstly, the combined tree suggests the basal branching pattern of *B. meyeri-johannis*, *B. mannii* and then *B. salaziensis*, while the molecular data set does not resolve the position of the latter two taxa. Secondly, the combined data suggests that there is a dichotomy between the Asian taxa and the Central American and South African taxa, whereas the molecular data shows a dichotomy between the Malesian and Tropical Chinese taxa and the rest of the Asian, Central American and South African taxa. Thirdly, the combined data suggests a closer relationship between *B. dipetala*, *B. floccifera* and the Malesian taxa. Fourthly, the combined data places *B oaxacana* at the base of the Central American and Andean taxa rather than as the sister taxon to *B. incarnata*. Finally, the combined data suggests a much closer relationship between the South American taxa, *B. sutherlandii* and *B. dregei*, and *B. gracilis* than the

molecular data alone which places these South African taxa at the base of the Central American and Andean clade.

	I_{MF}	I_M	P-value
morphology + molecules	0.147	0.4628	0.01
sequence + RFLPs	0.765	0.439	0.01

I values can range from 0 (perfect agreement between data sets) to 1 (no agreement). P-values of 0.05 or more indicate that the partition of data sets given in the left column is not significantly different from random, indicating congruence between data sets.

TABLE 3.6 INCONGRUENCY INDICES, I_{MF} AND I_M, AND P-VALUES FROM PARTITION-HOMOGENEITY TEST (PAUP* 4.0D60)

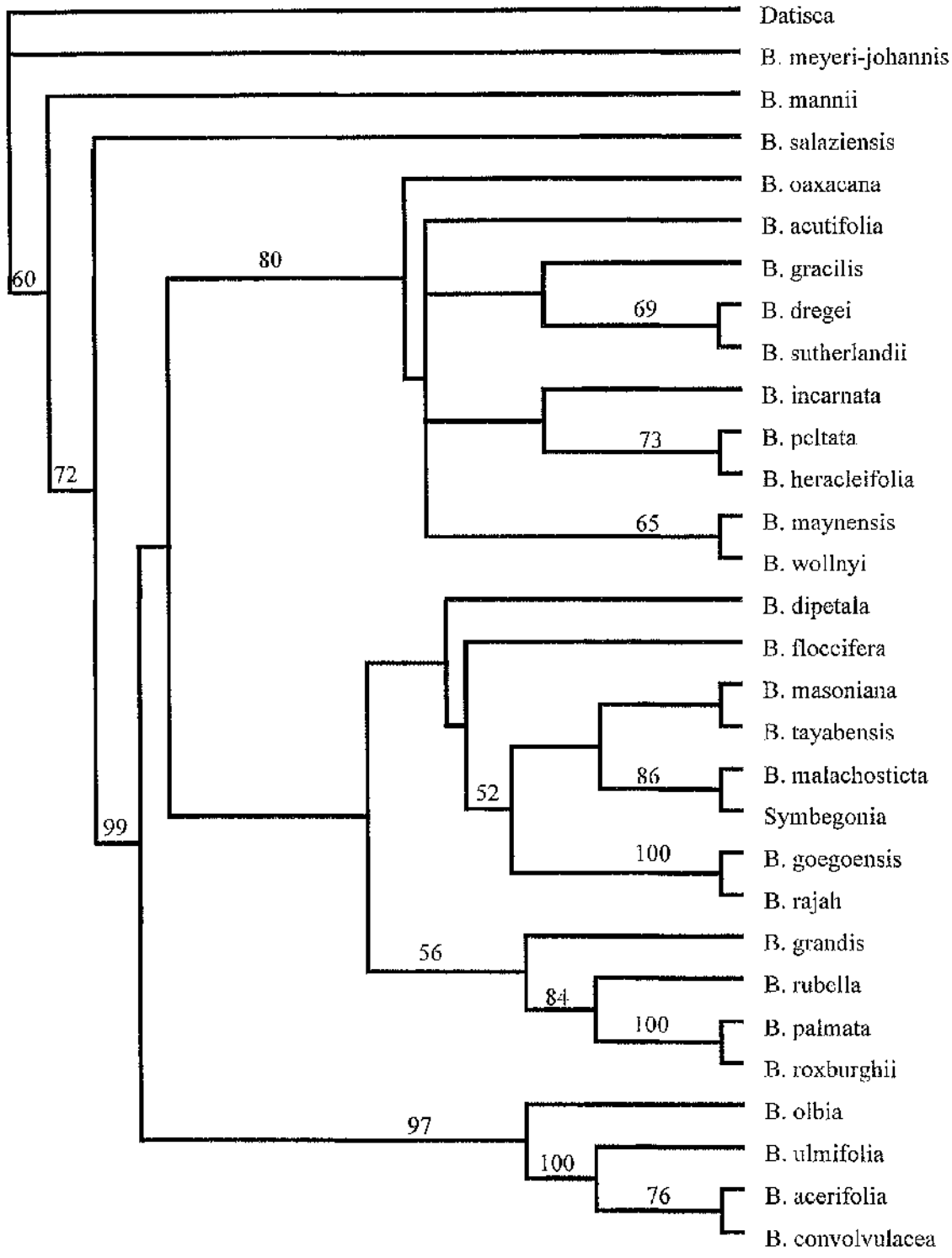


FIG. 3.9 STRICT CONSENSUS OF 4 EQUALLY MOST PARSIMONIOUS TREES OF 1302 STEPS (CI = 0.6813, RI = 0.5202) PRODUCED FROM THE CLADISTIC ANALYSIS OF *TRNC - TRND* SEQUENCE DATA (SUBSTITUTIONS AND INDELS) AND THE MORPHOLOGICAL DATA SET. NUMBERS INDICATE BOOTSTRAP SUPPORT.

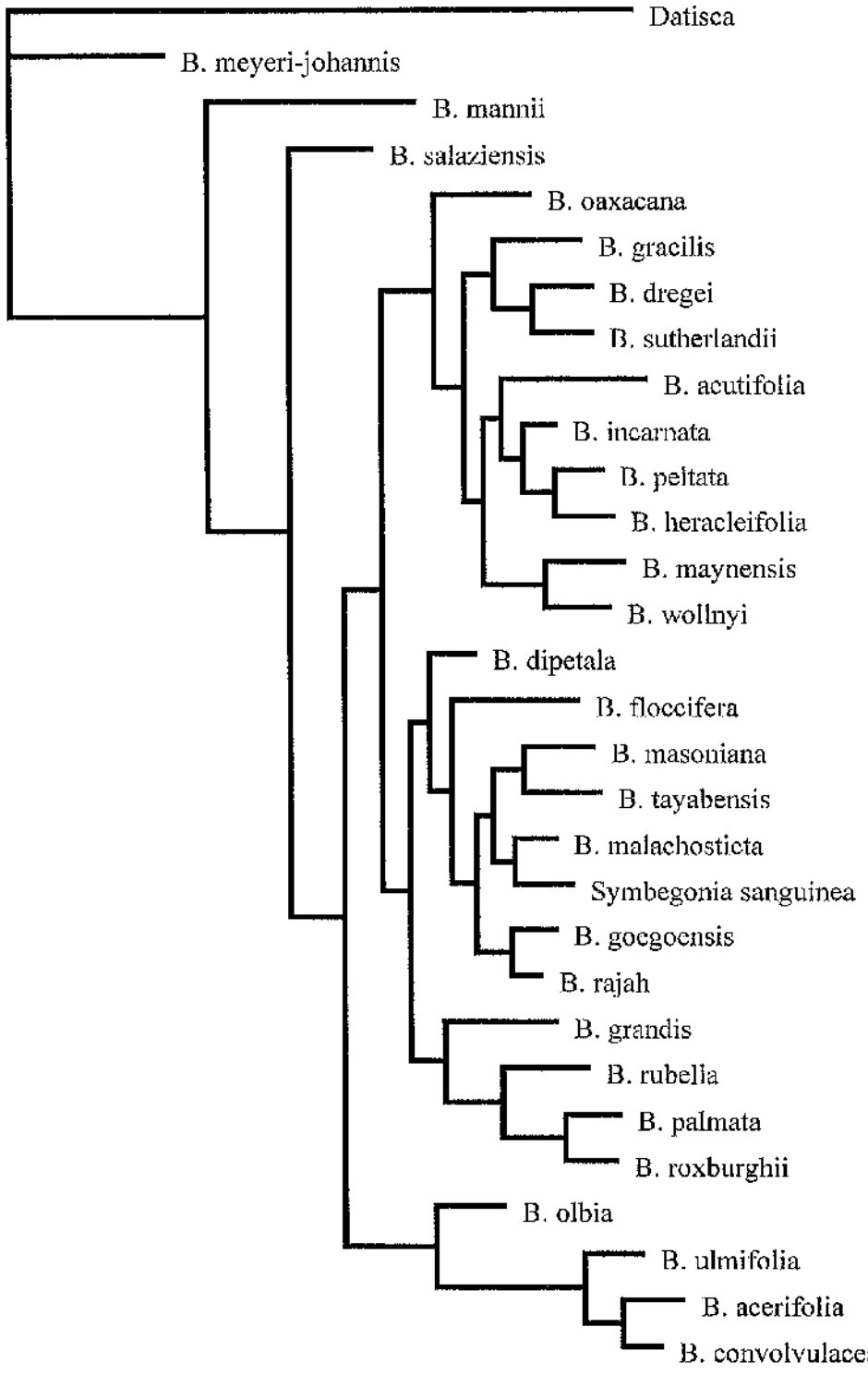


FIG. 3.10 ONE OF 4 EQUALLY MOST PARSIMONIOUS TREES OF 1302 STEPS (CI = 0.6813, RI = 0.5202) PRODUCED FROM THE CLADISTIC ANALYSIS OF *TRNC - TRND* SEQUENCE DATA (SUBSTITUTIONS AND INDELS) AND THE MORPHOLOGICAL DATA SET. BRANCH LENGTHS ARE PROPORTIONAL TO THE AMOUNT OF CHANGE OCCURRING ALONG THEM.

3.4 DISCUSSION

3.4.1 THE MONOPHYLY OF SECTION *KNESEBECKIA*

The molecular data strongly rejects the monophyly of section *Knesebeckia* and instead indicates that the section is polyphyletic (see fig 3.6). Within the American *Knesebeckia* this chloroplast phylogeny suggested that there are up to five different lineages. (1) *B. maynensis* and *B. wollnyi* group with *B. acutifolia* from section *Begonia*; (2) *B. gracilis*; (3) *B. oaxacana, B. incarnata, B. peltata* and *B. heracleifolia* (*B. peltata* groups with *B. heracleifolia* from section *Gireoudia*); (4) *B. olbia* is sister to the South American clade *ulmifolia-acerifolia-convolvulacea*; and (5) *B. acerifolia* occurs in a clade with *B. convolvulacea*. The clade containing the Central American *Begonia* (and South African *Begonia*) is supported by a 99% bootstrap value and a Bremer support value of six. The South American clade is supported by a bootstrap value of 100% and a Bremer support value of nine. The only Asian *Knesebeckia* sampled is *B. grandis* and this species occurs in a clade, supported by a bootstrap value of 84% and a Bremer support value of four, with species from sections *Trilobaria* (*B. rubella*), *Diploclinium* (*B. ravenii*), *Sphenanthera* (*B. roxburghii*) and *Platycentrum* (*B. aff. palmata*).

There are several important points which can be drawn from this data. *B. peltata* has been intermittently associated with section *Gireoudia* since de Candolle (1864) postulated its intermediate position between *Gireoudia* and *Knesebeckia* (see chapter 2, paragraph 2.4.4). Although the morphological analysis presented here does not place the two species in the same clade, *B. peltata* and *Gireoudia* share the following morphological characters: oblong anthers, three female tepals, an upright rhizomatous habit, persistent, ovate-lanceolate stipules and an extended peduncle. The chloroplast phylogeny presented here would appear to support the close relationship of these taxa, but further sampling from American *Knesebeckia* and section *Gireoudia* is required for confirmation.

Any future study of Central American *Knesebeckia* will require the inclusion of taxa from sections *Begonia*, *Gireoudia* and probably other American sections with a chromosome number of 2n = 28.

The occurrence of *B. acerifolia* in a clade with other South American species towards the base of the chloroplast phylogeny (see fig. 3.6), as presented here, may be anomalous. A much more comprehensively sampled analysis of the morphological data (see chapter 2) places *B. acerifolia* towards the base of a large clade containing species from American *Knesebeckia* and *Begonia*, while the morphological analysis presented here places *B. acerifolia* in a clade which also includes *B. incarnata*. This might suggest that the placement of this taxa is a reflection of the chloroplast phylogeny and not the species phylogeny and may be a result of introgressive hybridisation or lineage sorting (Doyle, 1992).

3.4.2 A PRELIMINARY ESTIMATE OF THE PHYLOGENY OF *BEGONIA*

As suggested by several authors (Arends, 1985; de Wilde, 1985; de Wilde & Arends, 1989; Van den Berg, 1985; Reitsma, 1984; 1985; de Lange & Bouman, 1985; 1992; Klazenga *et al.*, 1994) the African sections *Mezierea* and *Tetraphila* are closely related and section *Mezierea* is the most basal section in *Begonia*. The data presented here do not resolve the question of whether *Mezierea* is paraphyletic with respect to the other African sections and a more focused study will be required to answer this question. The basal position of section *Mezierea* is supported by parietal placentation and leathery / fleshy fruit (see chapter 2, paragraph 2.2.2.4).

Following the basal dichotomy of these fleshy fruited African *Begonia*, the clade of South American species includes taxa from Brazil, Venezuela and Ecuador. If the Ecuadorian species, *B. acerifolia*, is excluded (cf. paragraph 3.4.1), there appears to be a strong correlation between geography and phylogeny; these species are all from eastern South America. Species from the Andes (western South America) occur at the base of a

clade including Central American taxa. Although this may be a sampling artifact, it could be hypothesised that there are at least two lineages of *Begonia* in America, one occurring in tropical lowland, the other with a possible origin in the Andes and a migration north over the Isthmus of Panama into Central America and Mexico.

A significant finding of this research is that African *Begonia* are polyphyletic. Although no-one has seriously suggested that the species in sections *Rostrobegonia*, *Augustia*, *Peltaugustia* and *Sexalaria* are closely related to the fleshy fruited species in sections *Mezierea*, *Baccabegonia*, *Squamibegonia* and *Tetraphila*, their phylogenetic affinities have been unknown. Warburg (1894) suggested that *B. socotrana* may have affinities with southern Indian / Sri Lankan species placed in section *Reichenheimia* but de Lange and Bouman (1992) disagreed with this on the basis of their study of the seed morphology of these species. The chloroplast phylogeny places *B. sutherlandii* (*Rostrobegonia*) and *B. dregei* (*Augustia*) as the sister clade to the Andean and Central American species sampled here, supported by a 99% bootstrap value and a Bremer support value of 6. In the strict consensus of the molecular phylogeny, *B. floccifera* (a Southern Indian species in section *Reichenheimia*) is placed as the sister taxon to the clade of South African and Central American *Begonia*. This is an interesting result and supports, to a certain extent, Warburg's hypothesis. Further sampling may help resolve these relationships. It may be significant that these regions have all undergone periods of aridity. Sousa S. & Delgado S. (1993) have suggested that many Mexican legume lineages have Paleotropic relationships independent of South America, and Lavin & Sousa S. (1995) emphasised that phylogenetic analyses of North American tropical plant groups need to consider the potential Old World temperate, as well as Paleotropical, relatives in order to evaluate all potential sister group relationships.

It is interesting that there are two major independent lineages of *Begonia* in Asia. One, including *B. grandis*, the most northerly distributed *Begonia*, appears to occupy more subtropical and seasonal habitats; the other occurs in tropical southern China, the Philippines, Malaysia and Indonesia. This indicates more than one radiation of *Begonia*

in Asia. One possible hypothesis to explain this might be that one lineage entered Asia via the Middle East (see Tebbitt, 1997) and migrated through the Himalayas while the other lineage entered Asia via the rafting of the Indian subcontinent from Gondwanaland to Laurasia. It may be pertinent to note that *B. picta* is the most westerly distributed *Begonia* in Asia occurring in Pakistan and Western India as well as throughout the Himalayas. This species has several putatively primitive characters within Asian *Begonia*, such as branching trichomes on the fruit capsule (see chapter 4, paragraph 4.5.10).

The placement of *Symbegonia* in a clade with other Asian *Begonia* is perhaps not suprising. The morphological analysis places the species from section *Petermannia* as the sister group to *Symbegonia*. The distinctive morphological characters which have warranted the generic rank for *Symbegonia* are associated with an apparent change in pollination syndrome with tepals fused into a tube and the pollen with marked exine ornamentation (Van den Berg, 1983) (which would presumably make it more sticky). It is not known what pollinates any species in *Begonia* or *Symbegonia*. In overall form, *Symbegonia* species are very similar to species in *Petermannia*. The generic status of *Symbegonia* could be questioned.

3.4.3 THE CHARACTERISTICS OF NONCODING REGIONS OF CHLOROPLAST DNA

The rate of nucleotide substitution in noncoding regions appears to vary considerably. Pennington (1994) explored the utility of the noncoding region between the genes *rbc*L and *atp*β for a phylogenetic study of *Andira* but found insufficient variation. Detailed examination of the *rbc*L - *atp*β region revealed conserved promoter and ribosome binding sites and as a consequence of these features, the total rate of nucleotide substitution is about equivalent to that estimated for the *rbc*L coding region (Zurawski *et al.*, 1984; Zurawski & Clegg, 1987). Gielly & Taberlet (1994a) investigated the relative rates of substitution in the *trn*L intron and *trn*L - *trn*F spacer. Although it might

be expected that the rate of evolution in the intron is equivalent to that of protein gene evolution, as group I introns have conserved secondary structure and catalytic properties (Zurawski & Clegg, 1984; Clegg *et al.*, 1991; Gielly & Taberlet, 1994b), Gielly & Taberlet (1994b) found rates similar to that in the intergenic spacer and between 1.93 and 11.72 times faster than *rbc*L. This was explained by the hypothesis that the loop structures, which represent a large part of the sequence, are not subject to the same evolutionary constraints as the stems (Gielly & Taberlet, 1994b). Gielly & Taberlet (1994a) report that in some genera (e.g. *Fraxinus* and *Alnus*) they found very low variation in the *trn*L intron. This is similar to our data from *Begonia* (Tebbitt, 1997; Tebbitt & Badcock, unpublished data).

Whereas these two noncoding regions have been touted for utility at low taxonomic levels (e.g. Gielly & Taberlet, 1994b; Zurawski & Clegg, 1987), Goremykin *et al.* (1996) reported that the noncoding cpITS region of the inverted repeat evolved roughly six times more slowly than *rbc*L and was therefore useful in studying the evolution of land plants. This contradicts the earlier statements that noncoding regions of cpDNA tend to accumulate additions and deletions that eventually obliterate sequence similarity (Zurawski and Clegg, 1987), and so, for example, there is no sequence similarity between liverwort and tobacco noncoding regions (Wolfe & Sharpe, 1988). The inverted repeat of the chloroplast in general evolves more slowly than the large single copy region but it is not known why.

Many additions and deletions in noncoding regions involve short direct repeats that are likely to be the result of slipped-strand mispairing during replication. These short (indel) sequences, frequently two to about ten nucleotides (Takaiwa & Sugiura, 1982; Zurawski *et al.*, 1984; Zurawski & Clegg, 1987) appear to reoccur at nearly the same sites on a rapid time scale relative to the occurrence of nucleotide substitutions (Zurawski & Clegg, 1987). Due to the tendency of these small indels to cluster in "hot spot" regions (Kung *et al.*, 1982; Palmer *et al.*, 1988), the assignment of exact homology for each mutation may be difficult (Downie & Palmer, 1992). This has led to their exclusion in

some phylogenetic analyses (e.g. Sytsma & Gottlieb, 1986; Palmer *et al.*, 1988). Analyses of the evolution of noncoding regions suggest that length mutations occur at least as often as nucleotide substitution mutations among closely related taxa (Clegg *et al.*, 1991) and have proved useful in studies of closely related taxa (e.g. Doebley *et al.*, 1987; Soltis *et al.*, 1990).

Golenberg *et al.* (1993) analysed the occurrence of indels in the noncoding region *rbc*L - *atp*β for nine species of grasses, representing three tribes. They categorised the indels into Type Ia, Ib and Type II indels. Type Ia involves indels of short direct repeats of <10 bp and are frequently associated with runs of short direct repeats of one or two base motifs. Type Ib indels involve moderately sized regions of from four to over 40 bp and are distinguished from the first class by their more complicated nucleotide motifs. The majority of variation at these regions involves gains or losses of concatamers of sequences located either adjacent to or near the site of insertion/deletion, but may also involve palindromic sequences which can form hairpin structures. Type II indels represent all other indels. Golenberg *et al.* (1993) found that the phylogenetic tree based on the indel data represented a phylogenetic tree inconsistent with the accepted phylogeny of these nine grasses while the phylogenetic tree based on the nucleotide substitutions in this region was consistent with the accepted phylogeny. This finding is in contrary to the results, presented here, of the phylogenetic analysis of the indel data only (see paragraph 3.3.2.2). Of the 111 indel characters scored (see appendix M), 26 were parsimony informative, the analysis of which resulted in a tree largely congruent with the analysis of the substitution data but with higher consistency and retention indices.

Golenberg *et al.* (1993) stressed the homoplasy problems of parallel acquisition of indels in distantly related taxa and the repeat occurrence of indels at labile sites. Of course these problems are not unique to indel data sets and have been shown to occur in many sequence data sets with hot spots in nucleotide substitutions occurring within a gene (Ritland & Eckenwalder, 1992; M. Chase, presented at 1st biennial Systematics

Association meeting, Oxford, 1997). Another factor which needs to be considered is the occurrence of different rates of molecular evolution in different taxa, for example Gaut *et al.* (1992) demonstrated that the overall substitution rate for the *rbc*L locus of grasses is over five times the substitution rate in the *rbc*L of the palms; Bousquet *et al.* (1992) summarised several other examples of this phenomena in seed plants and Gaut *et al.* (1993) showed that this variation in nucleotide substitutions was not confined to the *rbc*L locus. The final concluding sentence of Gaut *et al.* (1993) states, "Taken together, the results [...] show that a cpDNA-based molecular clock is highly variable, both between major evolutionary lineages and between different cpDNA protein coding genes." Based on the data in this study and in those studies cited above, I would expand this statement to say that the variability in evolutionary rate is likely to include all regions of the chloroplast genome, both coding and noncoding.

With the *trn*L and *trn*C - *trn*D sequence data for *Begonia* and the studies of noncoding regions of the chloroplast cited here, it can be seen that noncoding chloroplast regions appear to have different evolutionary rates and can vary considerably in their utility at different taxonomic ranks, due to both their selective constraint and the molecular clock operating in that particular taxon. While Golenberg *et al.* (1993) cast doubt on the phylogenetic utility of indels in noncoding cpDNA, their case study utilised some grass genera which have been shown to have accelerated rates of nucleotide substitution; if indels occur at the same rate as nucleotide substitutions then there is an increased probability that homoplasy will be present in the indel data set of a group of closely related grass genera.

In the intergenic spacer region *trn*C - *trn*D, there did not appear to be a problem of homoplasy in the indel data set, as can be judged from the the high consistency and retention indices (CI = 0.8730; RI = 0.8161) (although indels due to length variation in SSRs were not scored); instead the biggest problem encountered was that of the alignment of *Begonia* sp. with the outgroup, *Datisca*. This was not simply a case of the indels obliterating sequence similarity (see Zurawski and Clegg, 1987), but was also due

to sequence divergence as judged by the nucleotide substitutions (see paragraph 3.3.2.1).

3.4.4 COMPARING THE RESULTS OF A PHYLOGENETIC ANALYSIS OF MAPPED RFLP DATA WITH SEQUENCE DATA FOR THE REGION *TRN*C - *TRN*D

While a detailed comparison of the RFLP data with the sequence data for the *trn*C - *trn*D region is not possible until the region has been fully sequenced, some preliminary conclusions can be made. Firstly, the analyses of both these data, although largely congruent, produce some discrepancies. Golenberg *et al.* (1993) suggest two factors which may restrict the impact of indels on phylogenetic inferences based on restriction fragment comparisons. First, indels of less than 100 bp (if they are in large fragments) may be below the level of resolution of agarose gels unless they involve the gain or loss of a restriction site. Second, labile sites where indels tend to reoccur may be the source of intraspecific polymorphisms, but also may be shared in distantly related species.

Until the *trn*C - *trn*D region is completely sequenced and the RFLP data of Tebbitt (1997) mapped accurately rather than relatively, the cause of the incongruence between the two data sets cannot be ascertained.

3.4.5 THE CONGRUENCE OF MOLECULAR DATA WITH MORPHOLOGICAL DATA

As demonstrated in paragraph 3.3.3, the morphological and molecular data sets are significantly incongruent. The Mickevich-Farris index of incongruence implies that 14.7 % of the total character incongruence is due to disparity between the two data sets, whereas the Miyamoto Index implies that 46% of the character incongruence is due to disparity between the two data sets. Pennington (1996) argued that these indices were a poor judge of incongruence and were somewhat subjective, with no statistical value designated as a cut off point. Agreeing with Donoghue and Sanderson (1992),

Pennington proposed that combining the data sets, irrespective of their incongruence and allowing the data sets to interact, would produce the best phylogenetic result. In fact, Pennington (1996) showed that the morphological and chloroplast restriction site data sets provided phylogenetic resolution at different hierarchical levels in *Andira*. However, Givnish & Sytsma (1997), while agreeing with Donoghue & Sanderson's (1992) view that morphological and molecular data have mutually complementary roles in the analysis of phylogenetic relationships, disagreed as to what those roles might be. Givnish & Sytsma (1997) proposed that morphological data are best suited for recognising species and suggesting broad patterns of relationships and that molecular data, due to their greater number and higher consistency of characters, are a more precise guide to detailed phylogenetic relationships barring any problems arising from hybridisation, introgression, and lineage sorting. The result of using molecular data to interpret morphological evolution would be the avoidance of circularity problems. These conclusions were partly made following their study of homoplasy in molecular and morphological data sets and the prediction of the likelihood of a correct phylogenetic inference from the different types of data.

Givnish & Sytsma (1997) showed that data sets with a low CI using few characters have a low likelihood of producing the correct phylogenetic inference while a data set based on a high number of characters and with a high CI gave a high likelihood of the correct phylogenetic inference. While these descriptors "high" and "low" are subjective, they might respectively be applied to the molecular and morphological data sets in this study. Givnish & Sytsma (1997) argue that morphological characters are more likely to be subject to the homoplasy sources of convergence and misclassification than are certain kinds of molecular characters.

With the preliminary nature of this morphological data set I would willingly admit that many of the characters may be misclassified. The homology of morphological character-states can often only be established by detailed comparative studies of organ development which are needed to exclude the possibility that (i) similar phenotypes are

merely convergent (analogous, not homologous); (ii) putatively alternative states of the same characters are actually states of different characters; or (iii) putatively different characters are not actually alternative states of the same character (Givnish & Sytsma, 1997).

The arguments for and against combining morphological and molecular data are complex and the advantages for both "total evidence" and avoidance of circularity in the study of morphological evolution can be appreciated. In the case of this study, the data sets are incongruent and I believe that more confidence can be placed in the molecular data (of course it must be remembered that this produces a chloroplast phylogeny and does not necessarily represent a phylogeny of the species (Doyle, 1992). With further study of homology assessment and the investigation of other sources of morphological characters, e.g. anatomy and micromorphology, morphological data will hopefully have more validity for combination with molecular data sets.

CHAPTER 4 TAXONOMIC TREATMENT

4.1 INTRODUCTION

The enigma of *Knesebeckia* is whether the section should contain species from more than one continent when all other sections of *Begonia* are limited to species from one continent. Is *Knesebeckia* monophyletic when species are included from Asia and America? In this review of the taxonomic history of *Knesebeckia*, I have recorded how different authors have treated this problem through the species they allocated to the section and their comments made when doing so. I have also investigated the nomenclatural problems encountered with respect to the species historically included in the section. The various taxonomic treatments included here are summarised in table 4.1.

4.2 A TAXONOMIC HISTORY OF *BEGONIA* SECTIONS *KNESEBECKIA* AND *DIPLOCLINIUM*

When Klotzsch monographed the Begoniaceae in 1854 he described 41 genera, including the four genera already recognised: *Begonia* L., *Eupetalum* Lindl., *Mezieria* Gaudich. and *Diploclinium* R. Wight. The citation by Klotzsch of R. Wight as the authority for *Diploclinium* appears to be the introduction of an error continued by authors to the present day. *Diploclinium* was included as a genus by Lindley in the first edition of his "The Vegetable Kingdom", validly published in 1846 by the inclusion of an analysis (Art. 42.3, ICBN). The generic name was used in the combination *Diploclinium Evansianum* (Andrews) Lindl. and this species should therefore be considered the type of the genus *Diploclinium*. *D. Evansianum* is now known as *Begonia grandis* Dryand. and has consistently been cited by authors as one of the prime examples of the Asian members of section *Knesebeckia* (Klotzsch) A.DC.

Klotzsch created a hierarchical system which has not been followed by any subsequent authors; he created two names of equal rank, Stephanocarpeae, distinguished by

persistent styles and Gymnocarpeae, with deciduous styles. Within the Stephanocarpeae, Klotzsch named two taxa of equal rank, Begoniaceae [sic] and Pritzelieae [sic], which were separated by the occurrence of a papillose band spiralling around the style branches in the former and the style branches being covered all over by papillae in the latter. The genus *Knesebeckia* was included in Begoniaceae, together with *Begonia*, *Saueria* Klotzsch, *Gaerdtia* Klotzsch, *Trendelenburgia* Klotzsch, *Ewaldia* Klotzsch, *Reichenheimia* Klotzsch, *Gurltia* Klotzsch, *Scheidweileria* Klotzsch, *Lepsia* Klotzsch, *Doratometra* Klotzsch, *Steineria* Klotzsch, *Pilderia* Klotzsch, *Mezierea*, *Rachia* Klotzsch, *Diploclinium* and *Mitscherlichia* Klotzsch.

The genus *Knesebeckia* Klotzsch was named in honour of his friend Freiherrn H. B. v. d. Knesebeck (Klotzsch, 1854, p. 161).

> "Dem Andenken meines verehrten Freundes, des Freiherrn. H. B. v. d. Knesebeck auf Faulenbenz bei Stargard in Pommern, eines um die Landwirthschaft sehr verdienten Mannes, Gewidmet."

Translation (Z. Badcock & H. Weitz):

> "In acknowledgement of my honoured friend Baron H. B. v. d. Knesebeck of Faulenbenz by Stargard in Pommern, dedicated to a very deserving man for agriculture."

Klotzsch described the genus as follows:

> Flores monoici. Masc. Petala 4 biserialia inaequalia, exteriora opposita majora suborbicularia, interiora minora, basi attenuata. Stamina plurima (28 - 60), filamenta in columnam cylindricam plus minus longam umbellatim connata, superne libera; antherae obovatae breves, apice orbiculato-tumidae extrorsae biloculares, loculi obliqui, apice subconniventes connectivi continui obtusi margini adnati longitudinaliter dehiscentes. Fem. petala 5 supera inaequalia pluriseriatim imbricata. Ovarium inferum trigonum triloculare trialatum. Ovula in

placentis e loculorum angulo centrali geminis conniventim-lamellatis, utrinque ovuliferis distincte pedicellatis creberrima, anatropa. Stylus persistens glaber trifidus, lobis bicruribus teretibus strictis divaricatis nec tortuosis, antice ad basin productis fascia papillosa semel-bis spiraliter torta continua cinctis. Capsula membranacea turbinato-triquetra trilocularis trialata, rarissime monoptera, alis inaequalibus, ad alarum originem per rimas arcuatas dehiscens. Semina innumerabilia minutissima oblonga reticulata exalbuminosa.

Frutices aut suffrutices Mexicanae et Guatemalenses. (Suffruticosi tuberosi saepe in foliorum axillis bulbiferi); foliis alternis petiolatis, basi oblique cordatis inaequilateris crenatis dentatis vel serratis subinde lobatis, nunquam peltatis; stipulis lateralibus scariosis deciduis; floribus cymosis pedunculatis axillaribus roseis; petalis interdum serratis aut dentatis.

This is translated as follows:

Flower monoecious. Male fl.: Petals 4 in two series, unequal, outer ones large, suborbicular, inner pair small, base attenuate. Stamens many (28 - 60), filaments fused umbellately into a ± long cylindrical column free above; anthers obovate, short, apex orbicular - thickened, 2 locules opening outwards, locules oblique, somewhat connivent at the apex, the connectives obtuse and continuous, adnate to the margin of the locules which dehisce longitudinally. Female fl.: petals 5, the upper ones unequal, overlapping in several series. Ovary inferior, 3 angled, 3 locular, 3 winged. Ovules on placentas (developing) as paired joined thin plates from the central angle of the locules, with each ovule-bearing surface distinctly pedicellate, the ovules very densely packed together, anatropous. Styles persistent, glabrous 3-cleft, each with the lobes 2-branched, terete, straight, spreading at a wide angle, not twisted, produced anteriorly at the base, encircled by a continuous papillose band which is twisted spirally about the legs once or twice. Capsule membranous, top shaped, 3-angled, 3-locular, 3 winged, very rarely with one

wing, wings unequal, dehiscing at the origin of the wings by curved cracks. Seeds innumerable, very minute, oblong, reticulate, exalbuminous.

Mexican & Guatemalan shrubs or subshrubs. Subshrubs tuberous, often with bulbils in the axils of the leaves; leaves alternate, petiolate, base obliquely cordate with unequal sides, crenate dentate or serrate to somewhat lobed, never peltate; stipules lateral, scarious, deciduous; flowers cymose, pedunculate, axillary, rose-coloured; petals sometimes serrate or dentate.

The 13 species included by Klotzsch in his treatment of the genus were as follows (the orthography of the names has been corrected in accordance with Art. 60.1, ISBN and authorities are cited according to Brummitt & Powell, 1992):

K. aucubifolia Klotzsch

B. aucubifolia Hort.

K. incarnata (Link & Otto) Klotzsch

B. incarnata Link & Otto

B. insignis Graham

K. papillosa (Graham) Klotzsch

B. papillosa Graham

K. discolor (R.Br.) Klotzsch

B. discolor R.Br.

B. evansiana Andrews

K. pedata (Liebm.) Klotzsch

B. pedata Liebm.

K. crenatiflora Klotzsch & Putzeys

K. biserrata (Lindl.) Klotzsch

B. biserrata Lindl.

K. ignea Warszewicz ex Klotzsch

K. falciloba (Liebm.) Klotzsch

B. falciloba Liebm.

K. bulbifera (Link & Otto) Klotzsch

B. bulbifera Link & Otto

K. martiana (Link & Otto) Klotzsch

B. martiana Link & Otto

B. diversifolia Graham

K. monoptera (Link & Otto) Klotzsch

B. monoptera Link & Otto

K. balmisiana (Ruiz ex Balmis) Klotzsch

B. balmisiana Ruiz, herb ex Balmis

All these species are from Mexico and Central America except *K. discolor* (=*B. grandis* Dryand.) which is from China. Although Klotzsch was aware of the Chinese origin of *K. discolor*, he did not substantiate the inclusion of the species in *Knesebeckia*, contrary to his generic description.

Alphonse de Candolle (1859) disagreed with Klotzsch's decision to create 41 genera where only four had existed previously and thus gave his circumscription of *Begonia* as "*Genera omnia Klotzsch (exceptis supra cit. et Mezierea).*", i.e. he placed all Klotzsch's genera in synonymy with *Begonia*, except *Casparya* and *Mezierea*. Despite this disagreement, de Candolle (1859) retained many of the genera named by Klotzsch as sections of *Begonia* e.g. "*Sectio Knesebeckia - Genus Kl.*"; thus *Knesebeckia* became a section of *Begonia* (1859, p. 125). Nine new species were included in *Begonia* L. section *Knesebeckia* (Klotzsch) A.DC., 1859. De Candolle (1859; 1864) used the name *Begoniastrum* A.DC. for *Begonia sensu* Klotzsch; this is a *nomen illegitimum* as it included the type of *Begonia*, *B. obliqua* L.

In de Candolle's *Prodromus* (1864) section *Knesebeckia* was described as follows:

Sect. XIII. KNESEBECKIA *Alph. DC. l.c. p.* 125. - Begoniae sp. *auct.* - Genus Knesebeckia *Kl. Beg. p. 41, t. 2, f. C.*

Fl. masc. Sepala 2. Petala 2. Staminum filamenta e columna centrali brevi aut toro valde convexo surgentia; antherae obovoideae, breves, obtusissimae. Fl. fem. Lobi 5 (rarius 4-3, in sp. asiat.). Styli 3, basi connati, superne bicrures, extus basi loborum inflati papillosi, papillis inde ad apicem obtusum loborum spiraliter adscendentibus. Ovarium 3-loculare. Placentae bipartae, undique ovuliferae. Capsula turbinato-triquetra, alis plus minus inaequalibus, stylis persistentibus coronata. - Herbae vel frutices, in Asia meridionali et America, praesertim in Mexico, crescentes; foliis in axilla plerumque bulbilliferis, saepius irregulariter dentato-lobatis. - Forma staminum constans. Numerus loborum fl. fem. in *B. Evansiana* variat et ideo species duas lobis 3, propter alios characteres et habitum, hic adjunexi.

This is translated as follows:

Male flower: sepals 2, petals 2; filaments of stamens arising from a short central column or a very convex torus; anthers obovoid, short, very obtuse. Pistillate flower: tepals five (more seldom three or four, in Asiatic species). Styles three, united at the base, in the upper part two-parted, outside at the base of the branches inflated and papillose, with the papillae spirally ascending from that point to the obtuse apex of the lobes. Ovary three-celled; placentas divided in two, bearing ovules all over. Capsule crowned with the persistent styles, top shaped, 3 sided, with more or less unequal wings. Herbs or shrubs, in Central Asia and America, chiefly in Mexico; leaves usually bearing bulbils in the axil, more often irregularly dentate-lobate. - Shape of the stamens constant. Number of lobes in the female flower in *B. Evansiana* varies and I have brought close to the same (*B. Evansiana*), two species with 3 lobes, on account of other characters and general habit.

De Candolle (1859 & 1864) agreed with Klotzsch that the section *Knesebeckia* should include species from the Americas and Asia. The taxa he included are listed below, with question marks where indicated by de Candolle.

Americanae

B. biserrata Lindl.

B. crenatiflora (Klotzsch & Putzey) A.DC.

B. ignea (Warszewicz ex Klotzsch) A.DC.

B. acerifolia Kunth ?

B. pedata Liebm.

B. anodifolia A.DC.

B. palmaris A.DC.

B. palmaris var. *jurgensenii* A.DC.

B. angustiloba A.DC.

B. balmisiana Ruiz ex Balmis

B. balmisiana var. *mitellifolia* A.DC.

B. monoptera Link & Otto

B. incarnata Link & Otto

B. incarnata var. *papillosa* (Graham) A.DC.

B. gracilis Humb., Bonpl. & Kunth

B. gracilis var. *depauperata* A.DC.

B. gracilis var. *membranacea* A.DC.

B. gracilis var. *nervipilosa* A.DC.

B. gracils var. *annulata* A.DC.

B. gracilis var. *martiana* (Link & Otto) A.DC.

B. gracilis var. *diversifolia* (Graham) A.DC.

B. dealbata Liebm.

B. maynensis A.DC.

B. faciloba Liebm.

B. bulbillifera Link & Otto

B. boissieri A.DC.

B. microcarpa A.DC.

B. oaxacana A.DC.

B. oaxacana var. *pilosula* A.DC.

Asiaticae

B. picta Sm.

B. evansiana Andrews

B. sinensis A.DC.

B. josephi A.DC.

B. josephi var. *macrocarpa* A.DC.

B. concanensis A.DC.

B. pedunculosa Wall.

Increasing the number of different ways that authors have treated the complex variation in Begoniaceae Bentham & Hooker (1867) recognised just two genera, *Begonia* and *Hillebrandia* D.Oliv., but within *Begonia* they included 5 unnamed series. Bentham & Hooker (1867) split some sections, e.g. *Diploclinium*, into more than one series.

> "Genus igitur Begoniam nostra sententia valde naturalem in integrum servavimus et sectiones Candolleanas cum generibus Klotzschianis in seriem forte nimis artificialem ordinavimus clavemque sequentem hic offerimus."

translated as:

> "Accordingly we have retained the genus *Begonia*, in our opinion, strongly natural in entirety and we have arranged the sections of de Candolle with the genera of Klotzsch, in a very strongly artificial series and we here offer the following key."

Series 2, which included section *Diploclinium p.p.*, was defined by:

"Filamenta libera v. monadelpha. Styli 3-4, integri, filiformes v. apices versus clavatus v. capitatas stigmatosi. Placentae integrae v. 2-partitae.-Species Africanae et Asiaticae."

translated as:

"Filaments free or monadelphous. Styles 3-4, entire, thread-like, clavate or capitate or stigmatiferous towards the apices. Placentae entire or 2-parted.-Species African and Asian."

Series 4, which included section *Knesebeckia,* was defined by

"Filamenta v. omnino v. alte in columnam apice v. sub apice antheriferam connata. Styli 2-lobi v. 2-partiti."

translated as:

"Filaments connate either throughout or in the upper part into a column bearing anthers at the apex or below the apex. Styles 2-lobed or 2-parted."

Series 5, which included sections *Begonia, Rachia* (Klotzsch) A.DC. and *Diploclinium p.p.*, was defined by

"Filamenta libera v. basi tantum connata. Styli saepissime 3, 2-fidi, v. 2-partiti."

translated as:

"Filaments free or fused only at base. Styles most often 3, 2-divided, or 2-parted."

In 1879 C. B. Clarke wrote the account of the Begoniaceae for the second volume of J. D. Hooker's *Flora of British India.* Section III of the Flora account was *Knesebeckia* and it was described as follows:

"Capsule 3-celled, triquetrous, the angles produced into three often unequal papery wings; faces with a rib or line down the middle; dehiscing by the falling

away of 2 or 3 of the faces; placentas 2-fid. Stamens very shortly monadelphous, anthers obovoid, connective not produced."

This section encompassed more variation than had previously been included in the section, as can be seen from the leads to the keys included in the account.

"A. Segments of female flower 5 (rarely 6), imbricate, inner smaller, innermost often smallest or 0. Sect. *Knesebeckia* A.DC."

"B. Segments of female flower 3, with sometimes a small fourth; two outer large, third small lateral. (*Trilobaria* A.DC.)"

Clarke therefore combined sections *Trilobaria* and *Knesebeckia*. Although Clarke made no mention of sections *Putzeysia* (Klotzsch) A.DC. and *Diploclinium*, the inclusion of *B. gemmipara* Hook.f., sole member of section *Putzeysia* and *B. cordifolia* Thwaites, included in the genus *Diploclinium* by Wight (1852), indicates that Clarke may have considered these to fall within the circumscription of his section *Knesebeckia*.

The taxa included under the first lead, A, were as follows:

B. picta Sm.

B. satrapis C.B.Clarke

B. evansiana Andr.

B. josephi A.DC.

B. josephi var. *typica*

B. josephi var. *macrocarpa* A.DC.

B. josephi var. *minima* C.B.Clarke

B. pedunculosa Wall.

B. surculigera Kurz

B. modestiflora Kurz

B. parvuliflora A.DC.

B. gemmipara Hook. f.

B. cordifolia (Wight) Thwaites

The species included under the second lead, B, were as follows:

B. amoena Wall.

B. scutata Wall.

B. ovatifolia A.DC.

B. subperfoliata Parish *ex* C.B.Clarke

B. moulmeinensis C.B.Clarke

B. fallax A.DC.

It should be noted that *B. concanensis* was not considered by Clarke to be in sect. *Knesebeckia* due to its often entire placentae and was instead placed in section *Uniplacentales* C.B.Clarke.

Clarke (1879) also described *B. khasiana* C.B.Clarke in the 'doubtful and excluded species' of his account. He treats *B. pedunculosa* Wall. Cat. 3672 B as a synonym of *B. khasiana*.

In 1881 Clarke published his ideas regarding the arrangement of the Indian species, believing that this could be applied to all *Begonia* species. He created six subgenera which appeared to him to be 'eminently natural'. These were based upon the dehiscence of the capsule as he was unable to attach high importance to the characters of the styles and stamens which were used previously by authors. These six subgenera were named: *Casparya* (Klotzsch) C.B.Clarke, *Parvibegonia* (A.DC.) C.B.Clarke, *Alaecida* (C.B.Clarke) C.B.Clarke, *Aschisma* C.B.Clarke, *Eu-Begonia* and *Platycentrum* (Klotzsch) C.B.Clarke. All the species included in sect. *Knesebeckia* by Clarke in the *Flora of British India* were included in the subgenus *Eu-Begonia*, with no other species.

When Warburg wrote the account of the Begoniaceae for Engler and Prantl's *Die Natürlichen Pflanzenfamilien* (1894), he took a different view to all those who had studied the family previously. While retaining the sectional treatment first established

for the family by Alphonse de Candolle (1859; 1864), Warburg disagreed that any sections should exist which included species from different continents. He therefore placed the Asiatic species of *Knesebeckia* into the Asiatic section *Diploclinium* Wight and the American species into section *Begoniastrum* A.DC. Within this enlarged section *Diploclinium*, Warburg also included *Trilobaria* A.DC., as in fact Clarke (1879) had done without the necessary nomenclature changes. Warburg included these taxa as subsections of *Diploclinium*, distinguishing them by the number of female perianth segments: subsection *Trilobaria* (A.DC.) Warb. with 3 female tepals, subsection *Eudiploclinium* Warb. with 4 female tepals and subsection *Knesebeckiopsis* Warb. with 5 female tepals. Three subsections, *Moschkowitzia* (Klotzsch) Warb., *Eubegonia* Warb. and *Euknesebeckia* Warb. were included within section *Begoniastrum* A.DC. *sensu* Warb. A further point is that Warburg placed *Rachia* as as subsection of *Magnusia* (Klotzsch) A.DC. alongside *Gireoudia* (Klotzsch) A.DC. and *Psathuron* A.DC.

Warburg's description of section *Diploclinium* is given below.

> Sect. XIX. Diploclinium Wight (als Gatt., incl. Sect. Trilobaria A. DC. und Knesebeckia A. DC. z. T.). Male: 4 (selten 2) Blhb., Stb. an der Basis verwachsen, A. obovat, Female: 3-5 Blhb., Gr. 3, bleibend, an der Basis verwachsen, 2lappig oder 2spaltig; Narbenpapillen ein continuierliches, oft schraubiges Band bildend; Samenleisten 2spaltig, Fr. mit 3 mehr oder weniger ungleichen Flügein. - Kräuter, fast immer mit knolligem Rhizom, stengellos oder mit meist kurzen dicken Stengeln, und handnervigen oder hand-fiedernervigen B. - Etwa 50 Arten in Asien; das Centrum der Verbreitung liegt im Osthimalaya und in Hinterindien, von wo sie einerseits durch den malayischen Archipel bis nach Neuguinea, anderseits durch die vorderindische Halbinsel nach Ceylon, endlich durch ganz China bis nach Japan hin ausstrahlen.
>
> § 1. *Trilobaria* A. DC., mit 3 Blhb. der female Bl.
>
> § 2. *Eudiploclinium* Warb., mit 4 Blhb. der female Bl.

§ 3. *Knesebeckiopsis* Warb. mit 5 Blhb. der female Bl. - *B. Evansiana* Andr. ist in verschieden Formen von Java bis Nordchina und Japan verbreitet, die übrigen Arten bewohnen begrenzte Gebiete. Mehrere Arten in Cultur, z. *B.* C. *picta* Sm. und *Evansiana* Andr., letzere vielfach zu Kreuzungen benutzt. - Vergl. A. DC. n. 93, 96, 98, 122-126, 136-141.

This is translated below:

Sect. XIX. *Diploclinium* Wight (as Genus, including sections *Trilobaria* and *Knesebeckia* A. DC. *pro parte*). Male: 4 (seldom 2) tepals, stamens at the base connate, anthers obovate. Female: 3-5 tepals, styles 3, persistent, fused at their base, 2 lobed or cleft; stigmatic papillae a continuous, often spiralling band; placentae 2 cleft. Fruit with 3 more or less unequal wings. - Herbs almost always with tuberous rhizomes, stemless or with very short thick stems and palmately veined or pinnately veined. About 50 species in Asia; the centre or the distribution lies in the East Himalaya and in Indochina from where, on the one hand, radiating through the Malay Archipelago to New Guinea, on the other hand, through the Indian subcontinent to Ceylon and finally throughout the whole of China as far as Japan.

§ 1. *Trilobaria* A. DC., with 3 tepals in the female flower.

§ 2. *Eudiploclinium* Warb., with 4 tepals in the female flower.

§ 3. *Knesebeckiopsis* Warb. with 5 tepals in the female flower. - *B. Evansiana* Andrews is distributed in diverse forms from Java to North China and Japan, the remaining species inhabit the defined area. Several species in cultivation such as *B. picta* Sm. and *Evansiana* Andrews, the latter often used in crosses. - See. A. DC. n. 93, 96, 98, 122-126, 136-141.

The next monograph of the Begoniaceae (and the most recent) was for the second edition of *Die Natürlichen Pflanzenfamilien* and was written by E. Irmscher (1925). He followed Warburg's account very closely; however, he did change Warburg's treatment

of section *Knesebeckia*. Irmscher believed that this grouping did warrant species which occurred on different continents being placed together; he therefore replaced the Asian members of section *Knesebeckia* while supporting the ranking of *Knesebeckia* as a subsection of *Begoniastrum*. This results in the subsection *Knesebeckia* remaining the only taxon to include species from more than one continent.

A translation of Irmscher's description is given below.

> Section *Begoniastrum* A.DC. extended (including *Moschkowitzia* Kl., *Begonia* Kl., *Knesebeckia* Kl.):
>
> Male: 4 (rarely 2) tep., filaments mostly free, more rarely fused below, anthers oblong, obtuse, as long as or longer than the filaments, connective scarcely projecting. Female: 5-6 (generally 5) tep., styles 3, persistent or falling, shortly fused below, bifid, style-branches often twisted, stigma forming a continuous helical band. Placentas bifid. Fruit 3 locular with 3 uneven wings. Mostly erect (rarely decumbent) herbs or sub-shrubs, never stem-less, with palmate-pinnate-veined or pinnate-veined, more rarely palmate-veined, mostly slanting and pointed leaves, without cystoliths, occasionally with tuberous stem-base and with small bulbils in the leaf axil. About 120 species in America, from Mexico and the Antilles as far as sub-tropical South America, as well as in Asia from India to China and Japan, and many of them in cultivation.
>
> § 1. *Moschkowitzia* Klotzsch (as genus). With 2 tep. in the male flowers. Belonging here *B. Wageneriana* Hook.f. in Venezuela.
>
> § 2. *Eubegonia* Warb. With 4 tep. in the male flowers; filaments mostly free; without tubers. A great number of species are cultivated, e.g. *B. semperflorens* Link et Otto, *B. suaveolens* Lodd., *B. ottonis* Walp., *B. nitida* Ait., *B. acuminata* Dryand., *B. pearcei* Hook.f., *B. scharffii* Reg., *B. schmidtiana* Reg., *B. humilis*, Hort. Kew, *B. hirtella* Link.

§ 3. *Knesebeckia* Kl. (as genus). With 4 tep. in the male flowers, filaments ± fused either throughout or in the upper part into a column; sometimes with tubers at the base of the stem, as well as with axillary bulbils. Belonging here e.g. *B. balmisiana* Ruiz., *B. gracilis* Kunth., *B. monoptera* Link et Otto, *B. incarnata* Link et Otto, *B. bulbillifera* Link et Otto, in Mexico, in addition Asiatic species, e.g. *B. pedunculosa* Wall. in India, *B. sinensis* A.DC. in China, *B. evansiana* Andr. distributed in many forms from Java to North China and Japan, the latter very much cultivated and used for hybridisation.

Irmscher placed section *Rachia* in synonymy with *Knesebeckia* in 1960.

In 1972 Baranov and Barkley published a change to the nomenclature of section *Begoniastrum*. They cited Art. 22 [=Art. 22, ICBN] for changing the name of section *Begoniastrum* A.DC., 1859, to section *Begonia nom. nov.* No reference was made to the position of the subsections included therein. Their changes and notes are given below.

"Section ***Begonia*** *nom. nov.*

Begonia Klotzsch, *loc. cit.*, 20, as genus.

Begoniastrum A.DC., *loc. cit.*, 31. 1859; *Prodromus* **15**, 1: 292. 1864, as section."

"The type species of this section would of course be *Begonia obliqua* L., *Species Plantarum*, 1056. 1753, except that Linnaeus placed three previously published species in his typical variety leaving the identity of the species questionable. *Begonia acutifolia* Jacq., *Collect.* 1: 122. 1786, is considered by the writers as the type species of the genus."

"Since the International Rules (Art. 22 [=Art. 22, ICBN] decree that the section including the type species of the correct name of the genus to which it is assigned bears the (generic) name unaltered as its epithet, the correct sectional epithet must be ***Begonia***."

This change only applies to de Candolle's section *Begoniastrum* and no mention is made of Irmscher's extended section *Begoniastrum*; therefore the necessary new combinations for the subsections as the delimitation of the section required then.

Also in 1972, Barkley and Baranov published a list of sections in *Begonia* with their types, allocating lectotypes where necessary. Here they list sections *Moschkowitzia* (Kl.) A.DC. and *Begoniastrum* A.DC. as synonyms of section *Begonia* but list *Knesebeckia* separately as a section in its own right, with the lectotype *B. incarnata* Link & Otto 1828. The citation of the authority of section *Diploclinium* in this paper is "*Diploclinium* (R. Wight 1852) A.DC." and the type is given as *B. cordifolia* Thwaites. Section *Rachia* is placed in synonymy with section *Gireoudia* A.DC. and the type of *Rachia* is cited as *B. lindleyana* Walpers, 1843 (*B. lanuginosa* A.DC., 1859) (see table 4.1 for a summary of this information).

In 1974 Baranov and Barkley published a further paper on the sections in *Begonia*, this time giving translations of the Latin descriptions of all the sections. Although they make no claims to any taxonomic and nomenclatural changes in this paper, there are some. Section *Rachia* is placed in synonymy with section *Knesebeckia* (not *Gireoudia*, as in 1972) and the type is cited as *B. incana* Lindl., 1841 (=*B. peltata* Otto & A.Dietr.).

Barkley and Golding published a list of all the species in the Begoniaceae in 1972, with a second edition in 1974. The second edition proposed to make corrections and some additions to their first edition. In this list all the species were placed in sections according to previous authors' decisions. Although both Asian and American species were placed in section *Knesebeckia* in these publications (Barkley and Golding, 1972; 1974), Asian and American species were also placed in section *Begonia*, contrary to any of the previous monographs of the genus.

Since the publication of this list of species, there has been an inconsistent use of the section names *Begonia* and *Knesebeckia*. In 1985 Burt-Utley, in a synopsis of the sections represented in Central America (p.125-128) in her monograph of the Central

American species in section *Gireoudia*, referred to section *Knesebeckia* and stated that *Knesebeckia* included "about 37 species in the Neotropics, with a concentration in Mexico, but the section is also poorly represented in the Far East". Wasshausen & Macellan (1995) used the name *Begoniastrum* when publishing a new species from Trinidad, contrary to Art. 22 of the ICBN. Chinese authors, e.g. Huang & Shui (1994) and Wu & Ku (1995; 1997) have used sect. *Begonia* rather than sect. *Knesebeckia* or sect. *Diploclinium* to which some of the species they described could have been designated.

Lindley (1846) (as genus)	Klotzsch (1854) (as genera)	de Candolle (1859; 1864) (as sections)	Bentham & Hooker (1867) (as series)	Clarke (1879) (as section)	Warburg (1894) (as sections or subsections)	Irmscher (1925)	Irmscher (1960)	Barkley & Baranov (1972) (as sections)	Baranov & Barkley (1974) (as sections)
Diploclinium	*Diploclinium*	*Diploclinium*	Series 2 & 5	*Knesebeckia* partly	*Diploclinium* subsection *Eudiploclinium*	*Diploclinium* subsection *Eudiploclinium*	n/a	*Diploclinium*	*Diploclinium*
n/a	*Putzeysia*	*Putzeysia*	Series 2	*Knesebeckia*	*Putzeysia*	*Putzeysia*	n/a	*Putzeysia*	*Putzeysia*
n/a		*Trilobaria*	Series 5	*Knesebeckia*	*Diploclinium* subsection *Trilobaria*	*Diploclinium* subsection *Trilobaria*	n/a	*Trilobaria*	*Trilobaria*
n/a	*Knesebeckia* (America & Asia)	*Knesebeckia* (America & Asia)	Series 4	*Knesebeckia*	*Diploclinium* subsection *Knesebeckiopsis* (Asian only) *Begoniastrum* subsection *Euknesebeckia* (American only)	*Begoniastrum* subsection *Knesebeckia* (America & Asia)	n/a	*Knesebeckia* (America & Asia)	*Knesebeckia* (America & Asia)
n/a	*Begonia*	*Begoniastrum*	Series 5	n/a	*Begoniastrum* subsection *Eubegonia*	*Begoniastrum* subsection *Eubegonia*	n/a	*Begonia*	*Begonia*
n/a	*Rachia*	*Rachia*	Series 5	n/a	*Magnusia* subsection *Rachia*	*Magnusia* subsection *Rachia*	*Knesebeckia*	*Gireoudia*	*Knesebeckia*
n/a	*Gireoudia*	*Gireoudia*	Series 5	n/a	*Magnusia* subsection *Gireoudia*	*Magnusia* subsection *Gireoudia*	n/a	*Gireoudia*	*Gireoudia*
n/a	*Magnusia*	*Magnusia*	Series 5	n/a	*Magnusia* subsection *Magnusia*	*Magnusia* subsection *Magnusia*	n/a	*Gireoudia*	*Gireoudia*
n/a	*Moschkowitzia*	*Moschkowitzia*	Series 5	n/a	*Begoniastrum* subsection *Moschkowitzia*	*Begoniastrum* subsection *Moschkowitzia*	n/a	*Begonia*	*Begonia*

TABLE 4.2 SUMMARY OF PREVIOUS TAXONOMIC TREATMENTS OF *BEGONIA* SECTION *KNESEBECKIA* AND *BEGONIA* SECTION *DIPLOCLINIUM*

4.3 TAXA INCLUDED IN *BEGONIA* SECTION *KNESEBECKIA SENSU* BARKLEY & GOLDING UP TO END OF 1997.

The list of American taxa given in 4.3.1 as members of section *Knesebeckia* are those cited as such in Barkley and Golding's (1974) list of species. It was not possible to review the literature effectively for citations of sections as many authors have used the section names *Begonia*, *Begoniastrum* and *Knesebeckia* synonymously. The authority, place and date of publication are cited. Names in italics are synonyms and follow Smith *et al.* (1986).

The list of Asian taxa listed in 4.3.2 are those cited as such in Barkley & Golding (1974) and by subsequent authors as belonging to section *Knesebeckia* or section *Begonia*. Types are cited for those Asian taxa not treated in this thesis and taxonomic changes made here have been incorporated into this list. Again, names in italics are synonyms and follow Smith *et al.* (1986), except for those changes made in this thesis. As has been shown in this thesis, the American and Asian taxa listed below in paragraphs 4.3.1 and 4.3.2 do not belong in the same section; the Asian taxa are in fact members of section *Diploclinium* Lindl. as *B. grandis* is the type of this section (see paragraph 4.1).

4.3.1 AMERICAN TAXA: SECTION *KNESEBECKIA*

acerifolia Humb., Bonpl. & Kunth, Nov. Gen. Sp. 7, folio 142, quarto 186, pl. 644, 1825. **Ecuador**

dolabrifera C.DC., Bull. Herb. Boissier II 8: 324, 1908; Smith & Wasshausen, Phytologia 44: 246, 1979.

acutiloba Liebm., Vid. Medd. Naturh. For. Kjöbenhavn 1852, p. 14, 1853; emend. L.B.Sm. & B.G.Schub., Contr. Gray Herb., 161: 28, pl. 3, 1946. **Mexico & Guatemala**

Knesebeckia acutiloba (Liebm.) Klotzsch ex Walpers, Ann. Bot. Syst. 4: 889, 1858.

angustiloba A.DC., Ann. Sci. Nat. Bot., sér. IV 11: 126, 1859. **Mexico**

dentata Pav. ex A.DC., Prodr. 15(1): 307, 1864, pro syn. *B. angustiloba* A.DC., 1859, *nom. inval.* (Art. 34.1(c)).

hicolor S.Watson, Proc. Amer. Acad. 22: 414, 1887; Irmscher, Bot. Jahrb. Syst. 50: 560, pl. 1, 1914; Smith & Schubert, Contr. Gray Herb. 154: 28, 1945.

anodifolia A.DC., Ann. Sci. Nat. Bot., sér. IV 11:126, 1859, "anodaefolia". **Mexico**

balmisiana Ruiz ex Balmis, Demonstr. 338, pl. 2, 1794 **Mexico**

populifolia Humb., Bonpl. & Kunth, Nov. Gen. Sp. 7, folio 142, quarto 185, pl. 643, 1825; Walpers, Ann. Bot. Syst. 44: 890, 1858; A. de Candolle, Prodr. 15(1): 308, 1864.

monoptera Link & Otto, Icon. Pl. Rar. 3: 27, pl. 14, 1828; W. J. Hooker, Bot. Mag. 64, pl. 3564, 1837; C. Karegeannes, Begonian 50: 9, 1983.

velutina Brongn. ex Neumann, Rev. Hort. II, 3: 218, pl., 1844, non hort. Vindob. ex Klotzsch, 1855, nec Parish ex Kurz, 1873; C. Karegeannes, Begonian 50: 11, 1983.

reniformis Pav. ex A.DC., Prodr. 15(1): 308, 1864, pro syn. *balmisiana* Ruiz ex Balmis, 1794, non Dryander, 1791; Smith & Schubert, Contr. Gray Herb., 154: 30, 1945; C. Karegeannes, Begonian 50: 9, 1983.

syphillitica Sessé & Mociño, Pl. Nov. Hisp. 162, 1890, "syphilitica"; Smith & Schubert, Contr. Gray Herb., 154: 27, 1941; C. Karegeannes, Begonian 50: 9, 1983.

Knesebeckia balmisiana (Ruiz ex Balmis) Klotzsch, Abh. Königl. Akad. Wiss. Berlin, 1854, p. 168, 1855; Begoniac. 48, 1855; A. de Candolle, Prodr. 15(1): 308, 1864.

Knesebeckia monoptera (Link & Otto) Klotzsch, Abh. Königl. Akad. Wiss. Berlin, 1854: 168, 1855; Begoniac. 48, 1855; A. de Candolle, Prodr. 15(1): 308, 1864; C. Karegeannes, Begonian 50: 10, 1983.

balmisiana var. **mitellifolia** A.DC., Prodr. 15(1): 308, 1864. **Mexico**

biserrata Lindl., J. Hort. Soc. London, 2: 313, 1847; W. J. Hooker, Bot. Mag. 79, pl. 4746, 1853. **Mexico & Guatemala**

Knesebeckia biserrata (Lindl.) Klotzsch, Abh. Königl. Akad. Wiss. Berlin, 1854: 165, 1855; Begoniac. 48, 1855; A. de Candolle, Prodr. 15(1): 305, 1864.

Knesebeckia crenatiflora Klotzsch & Putz., Abh. Königl. Akad. Wiss. Berlin, 1854, p. 165, 1855; Begoniac. 45, 1855; A. de Candolle Prodr. 15(1): 306, 1864; Smith & Wasshausen, Phytologia 54: 466, 1984; Phytologia 55: 112, 1984.

palmaris A.DC., Ann. Sci. Nat. Bot. sér. IV, 11: 126, 1859; Smith & Schubert, Contr. Gray Herb. 154: 28, 1945

palmaris var. *jurgensenii* A.DC., Prodr. 15(1): 307, 1864; Smith & Schubert, Contr. Gray Herb., 154: 28, 1945.

crenatiflora (Klotzsch & Putz.) A.DC., Prodr. 15(1): 306, 1864; Smith & Wasshausen, Phytologia 54: 466, 1984.

palmata Pav. in herb. Boiss., ex A.DC. Prodr. 15(1): 307, 1864, non D. Don 1825, pro syn. *B. palmaris* A.DC., 1859, nom. inval. & illegit.; Smith & Schubert, Contr. Gray Herb. 154: 28, 1945.

palmata Sessé & Mociño, Pl. Nov. Hisp. 163, 1890, non D. Don 1825; Smith & Schubert, Contr. Gray Herb. 154: 27, 1945.

biserrata var. **glandulosa** L.B.Sm. & B.G.Schub., Contr. Gray Herb. 154: 23, 1945. **Mexico**

boissieri A.DC., Ann. Sci. Nat. Bot., sér. IV, 11: 126, 1859; Prodr. 15(1): 311, 1864; Smith & Schubert, J. Wash. Acad. Sci. 40: 241, pl. 1a, 1950. **Mexico**

abaculoides Ziesenh., Begonian 35: 257, 1968; Begonian 36: 39, 1969; Smith & Wasshausen, Phytologia 52: 441, 1983.

suffruticosa Pav. ex A.DC., Prodr. 15(1): 311, 1864, non Meisn., 1840, pro syn. *B. boissieri* A.DC., 1864.

bulbillifera Link & Otto, Icon. Pl. Rar. 89, pl. 45, 1831. **Mexico**

bulbifera Loddiges ex Otto & A.Dietr., Allg. Gartenzeitung 9: 59, 1841, sphalmate pro *bulbillifera* Link & Otto, 1831.

tuberosa Pav. ex A.DC., Prodr. 15(1): 311, 1864, pro syn. *B. bulbillifera* Link & Otto, 1831, non Lamarck, 1795.

Knesebeckia bulbifera (Link & Otto) Klotzsch, Monatsber. Königl. Preuss. Akad. Wiss. Berlin, 122, 1854; Abh. Königl. Akad. Wiss. Berlin, 1854: 167, 1855; Begoniac. 47, 1855, sphalmate pro *bulbillifera* Link & Otto, 1831; A. de Candolle, Prodr. 15(1): 311, 1864.

cebadillensis Houghton in Standl. & Calderón, Lista Prelim. Pl. Salvador 156, 1925, *nomen nudum*; Houghton ex L.B.Sm. & B.G.Schub., Contr. Gray Herb. 161: 26, pl. 3, 1946. **Central America**

cuernavacensis Ziesenh., Begonian 26: 9, pl., 1959. **Mexico**

dealbata Liebm., Vid. Medd. Naturh. For. Kjöbenhavn 1852, p. 5, 1853. **Mexico**

dichroa Sprague, Bull. Misc. Inform. 251, 1908; T. A. Sprague, Bot. Mag. 138, pl. 8412, 1912. **Brazil**

falciloba Liebm., Vid. Medd. Naturh. For. Kjöbenhavn 1852, p. 15, 1853; Smith & Schubert, Contr. Gray Herb., 165: 91, pl. 1, 1947. **Mexico & Guatemala**

Knesebeckia falciloba (Liebm.) Klotzsch, Abh. Königl. Akad. Wiss. Berlin, 1854: 166, 1855; Begoniac. 46, 1855; A. de Candolle, Prodr. 15(1): 311, 1864.

fernaldiana L.B.Sm. & B.G.Schub., Contr. Gray Herb. 165: 93, 1947. **Mexico**

gracilis Humb., Bonpl. & Kunth, Nov. Gen. Sp. 7, folio 141, quarto 184, 1825. **Mexico**

gracilis var. **annulata** A.DC., Prodr. 15(1): 309, 1864.

gracilis var. **depauperata** A.DC., Prodr. 15(1): 309, 1864.

gracilis var. **diversifolia** A.DC., Prodr. 15(1): 310, 1864.

diversifolia Graham, Edinburgh New Philos. J. 22: 183, 1830; Bot. Mag. 57, pl. 2966, 1830; Liebmann, Vid. Medd. Naturh. For. Kjöbenhavn 1852, p. 4, 1853; A. de Candolle, Prodr. 15(1): 310, 1864.

diversifolia Knowles & Westc., Fl. Cab. 1: 27, pl. 14, 1837; Smith & Wasshausen, Phytologia 54: 466, 1984.

gracilis var. **martiana** (Link & Otto) A.DC., Prodr. 15(1): 309, 1864.

Totoncaxoxo coyollin Hernandez, Nova Plantarum Animalium et Mexicanarum Historia, 195, 1651; Sessé & Mociño, Pl. Nov. Hisp. 162, 1890; Smith & Schubert, Contr. Gray Herb. 154: 27, 1945.

martiana Link & Otto, Ic. Pl. Rar. 5: 49, pl. 25, 1829.

heterophylla hort. Schoenbr. ex Klotzsch, Monatsber. Königl. Preuss. Akad. Wiss. Berlin, 122, 1854, pro syn. *Knesebeckia martiana* (Link & Otto) Klotzsch, 1854; A. de Candolle, Prodr. 15(1): 310, 1864.

Knesebeckia martiana (Link & Otto) Klotzsch, Monatsber. Königl. Preuss. Akad. Wiss. Berlin, 122, 1854; Abh. Königl. Akad. Wiss. Berlin, 1854, p. 167, pl. 2C, 1855; Begoniac. 47, pl. 2C, 1855; A. de Candolle, Prodr. 15(1): 310, 1864.

bulbillifera Moric. ex A.DC., Prodr. 15(1): 310, 1864, non Link & Otto, 1831, pro syn. *gracilis* var. *martiana* (Link & Otto) A.DC., 1864.

tuberosa Sessé & Mociño, Pl. Nov. Hisp. 163, 1890; Fl. Mexico, ed. 2: 218, 1894; Smith & Schubert, Contr. Gray Herb. 154: 27, 1945.

gracilis var. **membranacea** A.DC., Prodr. 15(1): 309, 1864.

gracilis var. **nervipilosa** A.DC., Prodr. 15(1): 309, 1864.

ignea (Warszewicz ex Klotzsch) A.DC., Prodr. 15(1): 306, 1864. **Guatemala**

Knesebeckia ignea Warszewicz ex Klotzsch, Abh. Königl. Akad. Wiss. Berlin, 1854, p. 166, 1855; Begoniac. 46, 1855; A. de Candolle Prodr. 15(1): 306, 1864.

ignea var **tuberosa** C.DC., Bull. Soc. Roy. Bot. Belgique 35: 267, 1896. **Costa Rica**

incarnata Link & Otto Icon Pl. Rar. 4: 37, pl. 19, 1829. **Mexico**

aucubifolia hort. ex Klotzsch, Monatsber. Königl. Preuss. Akad. Wiss. Berlin, 122, 1854, "*aucubaefolia*," pro syn. *Knesebeckia aucubifolia* Klotzsch, 1854; A. de Candolle, Prodr. 15(1): 309, 1864.

ciliata hort ex Steud., Nom. Bot., ed. 2 1: 193, 1840, pro syn. *insignis* Graham, 1829, non Humb., Bonpl. & Kunth, 1825; Walpers, Repert. Bot. Syst. 2: 213, 1843.

insignis Graham, Edinburgh New Philos. J. 11, 1929; Bot. Mag. 56, pl. 2900, 1829; Walpers, Repert. Bot. Syst. 2: 213, 1843.

martiana sensu Schlechtendal, Linnaea 5: 604, 1830, non Link & Otto, 1829; A. de Candolle Prodr. 15(1): 309, 1864.

subpeltata hort. ex Regel, Gartenflora 15: 358, 1866, non Wight 1852; Irmscher, Pareys Blümengartnerei, ed. 2: 89, 1960.

Knesebeckia aucubifolia hort. Berol. ex Klotzsch, Monatsber. Königl. Preuss. Akad. Wiss. Berlin, 122, 1854, "*aucubaefolia*,"; Abh. Königl. Akad. Wiss. Berlin, 1854: 162, 1855; Begoniac. 42, 1855; A. de Candolle Prodr. 15(1): 309, 1864.

Knesebeckia incarnata (Link & Otto) Klotzsch, Monatsber. Königl. Preuss. Akad. Wiss. Berlin, 122, 1854; Abh. Königl. Akad. Wiss. Berlin, 1854, p. 163, 1855; Begoniac. 43, 1855; A. de Candolle Prodr. 15(1): 309, 1864.

incarnata var. **papillosa** A.DC., Prodr. 15(1): 309, 1864. **Mexico**

papillosa Graham, Bot. Mag. 55, pl. 2846, 1828; A. de Candolle Prodr. 15(1): 309, 1864.	
Knesebeckia papillosa (Graham) Klotzsch, Monatsber. Königl. Preuss. Akad. Wiss. Berlin, 122, 1854; Abh. Königl. Akad. Wiss. Berlin, 1854, p. 163, 1855; Begoniac. 43, 1855; A. de Candolle Prodr. 15(1): 309, 1864.	
kellermanii C.DC., Smithsonian Misc. Coll. 69(12): 1, 1919; Smith & Schubert, Fieldiana, Bot. 24: 177, 1961; J. Golding, Phytologia 47: 293, 1981.	**Guatemala**
ludwigii Irmsch., Biblioth. Bot. 116: 113, 1937.	**Ecuador**
ecuador E.K.Gray, Begonias 16, 1931, "ecquador"; F. Carrell, Begonian 17: 128, 1950; Smith et al., Smithsonian Contr. Bot. 60, 1986.	
ecuadorensis hort. ex Everett, J. New York Bot. Gard. 41: 18, 1940, non Buxton, 1932; A. Clarke, Begonian 14: 150, 1947; F. Carrell, Begonian 17: 128, 1950.	
rigida sensu A.Clark, Begonian 14: 150, pl., 1947; F. Carrell, Begonian 17: 128, 1950.	
macdanielsii Standl., Fieldiana, Bot. Ser. 17: 266, 1937.	**Mexico**
maynensis A.DC., Ann. Sci. Nat. Bot. sér. IV 11: 126, 1859.	**N. Andes**
michoacana L.B.Sm. & B.G.Schub., Contr. Gray Herb. 165: 94, 1947.	**Mexico**
mucronistipula C.DC., Smithsonian Misc. Collect. 69(12): 3, 1919.	**Panama**
nemoralis L.B.Sm. & B.G.Schub., Contr. Gray Herb. 165: 93, 1947.	**Mexico**
oaxacana A.DC., Ann. Sci. Nat. Bot. IV, 11: 127, 1859.	**Mexico**
luxii C.DC., Bot. Gaz. 20: 541, 1895; Smith & Schubert, Ann. Missouri Bot. Gard. 45: 58, 1958.	**Central America**

luxii var. *pilosior* C.DC., Bull. Soc. Roy. Bot. Belgique 35: 266, 1896; Standley, Filediana, Bot. Ser. 18: 743, 1937; Smith & Schubert, Ann. Missouri Bot. Gard. 45: 58, 1958.

serrulatoala C.DC., Bull. Herb. Boissier, II, 8: 321, 1908; Smith & Schubert, Ann. Missouri Bot. Gard. 45: 58, 1958.

pubipedicella C.DC. Smithsonian Misc. Collect. 69(12): 7, 1919; Smith & Schubert, Ann. Missouri Bot. Gard. 45: 58, 1958.

oaxacana var. pilosula A.DC., Ann. Sci. Nat. Bot. IV 11: 127, 1859; Smith & Schubert, Ann. Missouri Bot. Gard. 45: 58, 1958. **Mexico**

plagiata Linden ex A.DC., Prodr. 15(1): 312, 1864, pro syn. *oaxacana* var. *pilosula* A.DC., 1859, nom. inval. (Art. 34.1 (c)); Smith & Schubert, Ann. Missouri Bot. Gard. 45: 58, 1958.

oaxacana var. stenoptera L.B.Sm. & B.G.Schub., Fieldiana, Bot. 24: 177, 1961. **Costa Rica & Panama**

stenoptera C.DC., Smithsonian Misc. Collect. 69(12): 2, 1919; Smith & Schubert, Fieldiana: Bot. 24: 177, 1961.

olbia Kerch., Rev. Hort. Belge Étrangère 9: 241, pl., 1883. **Brazil**

platanifolia Schott var. *ohlendorffiana* Rchb.f., Gard. Chron., n.s. 10: 780, 1878; Irmscher, Pareys Blümengartnerei, ed. 2: 89, 1960.

pedata Liebm., Vid. Medd. Naturh. For. Kjöbenhavn 1852, p. 10, 1853. **Mexico**

Knesebeckia pedata (Liebm.) Klotzsch, Abh. Königl. Akad. Wiss. Berlin, 1854, p. 164, 1855; Begoniac. 44, 1855; A. de Candolle, Prodr. 15(1): 306, 1864.

Knesebeckia crenatiflora sensu L.B.Sm. & Wassh., Phytologia 54: 472, 1984, non Klotzsch & Putz., 1855.

peltata Otto & A.Dietr., Allg. Gartenzeitung, 9: 58, Feb. 1841; Alexander, Addisonia, 23(4): 53, pl. 763, 1959; Smith & Schubert, Fieldiana, Bot. 24(1): 177, 1961; J. Golding, Phytologia 47: 291, 1981. **Mexico & Guatemala**

incana Lindl., Bot. Reg. 27 (misc.): 39, May 1841; J. Golding, Phytologia 47: 291, 1981.

Rachia peltata (Otto & A.Dietr.) Klotzsch, Monatsber. Königl. Preuss. Akad. Wiss. Berlin, 124, 1854; Abh. Königl. Akad. Wiss. Berlin, 1854, p. 189, pl. 6B, 1855; Begoniac. 69, pl. 6B, 1855; A. de Candolle, Prodr. 15(1): 326, 1864; J. Golding, Phytologia 47: 292, 1981.

peltata var. **auriformis** (Van Houtte ex Klotzsch) Golding, Phytologia 47: 292, 1981. **Mexico**

auriformis Van Houtte ex Klotzsch, Monatsber. Königl. Preuss. Akad. Wiss. Berlin, 24, 1854; Abh. Königl. Akad. Wiss. Berlin 1854: 189, 1855; Begoniac. 69, 1855, pro syn. *Rachia auriformis* Klotzsch, 1854; A. de Candolle, Prodr. 15(1): 327, 1864; J. Golding, Phytologia 47: 292, 1981.

Rachia incana (Lindl.) Klotzsch, Abh. Königl. Akad. Wiss. Berlin, 1854, p. 189, 1855; Begoniac. 69, 1855; A. de Candolle Prodr. 15(1): 326, 1864; J. Golding, Phytologia 47: 292, 1981.

incana var. *auriformis* (Van Houtte ex Klotzsch) A.DC., Prodr. 15(1): 327, 1864; J. Golding, Phytologia 47: 292, 1981.

sandtii Ziesenh., Begonian 36: 184-186, pl., 1969. **Mexico**

uniflora S.Watson, Proc. Amer. Acad. 25: 149, 1890. **Mexico**

tayloriae Standl. ex herb. F.A.Barkley 1969, ined.; Standl. ex F.A.Barkley & Golding, Sp. Begoniaceae, ed. 2: 127, 1974, *nomen nudum*.

uruapensis Sessé & Mociño, Pl. Nov. Hisp. 162, 1890; Fl. Mexico, ed. 2: 219, 1894. **Mexico**

asteroides L.B.Sm. & B.G.Schub., Contr. Gray Herb. 127: 30, 1939; Smith & Schubert, Contr. Gray Herb. 154: 31, 1945.

uruapensis var. **rosei** L.B.Sm. & B.G.Schub., Contr. Gray Herb. 154: 26, 1945.

weberlingii Irmsch., Beitr. Biol. Pflanzen. 39: 438, pl. 1, 1963. **El Salvador**

wollnyi Herzog, Repert. Spec. Nov. Regni Veg. 7: 63, 1909. **Brazil &**

acrensis Irmsch., Bot. Jahrb. Syst. 74: 605, 1949; Smith & Schubert, Revista Univ. (Cuzco) 33(87): 84, 1944; Smith & Schubert, J. Wash. Acad. Sci. 45: 114, 1955; Smith et al., Smithsonian Contr. Bot. 60: 250, 1986. **Bolivia**

williamsii Rusby & Nash, Torreya, 6: 47, pl., 1906, nom. illegit. non × *williamsii* B.S. Williams, 1882; Smith & Schubert, Revista Univ. (Cuzco) 33(87): 84, 1944; Smith et al., 1986.

4.3.2 ASIAN TAXA: SECTION *DIPLOCLINIUM* (LINDL.) A.DC. *PRO PARTE*

adscendens C.B.Clarke "*ascendens*", J. Linn. Soc. Bot. 25: 26, pl. 13, 1890. **India, Burma**

alveolata T.T.Yu, Bull. Fan. Mem. Inst. Biol., n.s. 1: 121, 1948. **China**

SE Yunnan, Pingbien, Timi, 1500 m, under woods, moist place, 13.xi.1939, *C. W. Wang* 82780 (holotype: KUN); Ma-li-pi, Gwan-gao, 1000 m, under woods on rocks, 10.ii.1940, *C. W. Wang* 86714 (paratype).

anceps Irmsch., Notes Roy. Bot. Gard. Edinburgh 21:35, 1951. **China**

Yunnan, Ma-li-po, Gwan-gao, 1000 m., under woods on rocks, *C. W. Wang* 86714, 10.ii.1940 (holotype: KUN).

asperifolia Irmsch., Mitt. Inst. Allg. Bot. Hamburg 6: 359, 1927. **China**

asperifolia var. **tomentosa** T.T.Yu, Bull. Fan. Mem. Inst. Biol., n. s. 1: 118, 1948. **China**

cehengensis T.C.Ku, Acta Phytotax. Sin. 33(3): 254, 1995. **China**

Guizhou, Ceheng, Huarong, 750 m. 1.xi.1958, *Z. Y. Cao* 1258 (holotype: PE).

clavicaulis Irmsch., Mitt. Inst. Allg. Bot. Hamburg 10: 500, 1939. **China**

Yunnan, hills around Lung-fan, 25° 54' N, 98° 33' E, 7000 ft, margins of and in shady thickets, Aug. 1925, *G. Forrest* 27158 (syntypes: E, K).

dentatobracteata C.Y.Wu, Acta Phytotax. Sin. 33(3): 254, 1995. **China**

Yunnan: Pianma, 1900 m, in broad-leaved forests, 28.vii.1978, *S. K. Wu* 1429 (holotype, KUN); ibidem, Gangfang, alt. 1600 m, on shady stony cliffs, 19.ii.1939, *F. Kingdon Ward* 326 (paratype: A), "dentato-bracteata" (Art. 60.9 ICBN).

fimbristipula Hance, J. Bot. 21: 202, 1883. **China**

cyclophylla Hook. f., Bot. Mag. 113., pl. 6926, 1887.

flagellaris H.Hara, J. Jap. Bot. 48 (12): 358, 1973. **Nepal**

C. Nepal, Gul Bhanjang - Latsu, 2300-2400 m, 29.viii.1972, *Kanai, Hara & Ohba* 723648 (holotype: TI); Phulchauki, 2200-2770 m, 9.viii.1969, *Kanai et al.* 673396 (paratype: TI); Chipling - Ingyur, 2160-2440 m, 21.viii. 1969, *Kanai & Malla* 673598 (paratype: TI); Duche Gyang - Thodang Danda, 2250-2470 m, 22.viii.1969, *Malla & Kanai* 674633 (paratype: TI)

fordii Irmsch., Mitt. Inst. Allg. Bot. Hamburg 10: 501, 1939 **China**

Kwangtung, North-west River, Aug. 1890, *Ford* 238 (holotype: K).

glechomifolia C.M.Hu ex C.Y.Wu & T.C.Ku, Acta Phytotax. Sin. 33(3): 255, 1995. **China**

Guangxi, Jinxiu, 27.6.1934, *S. S. Sin* 23336 (holotype: IBSC), *S. S. Sin* 23076 (paratype); Xiangzhou. 1000 m, on rocks, 18.6.1936, *Z. Huang* 39390(paratype).

grandis Dryand., Trans. Linn. Soc. 1: 163, 1791. **China**

Sjukaido Kaempfer, *Amoen. Exot. Fasc.* 5: 888, 1712, nom. inval.

obliqua sensu Thunberg, Fl. Jap. 231, 1784, non L., 1753.

evansiana Andrews, Botanist's Repository 10, pl. 627, June 1811.

discolor R.Br., in Aiton, Hort. Kew, ed. 2, 5: 284, 1813.

bulbifera hort. ex Steudel, Nom. Bot. 1: 104, 1821, pro syn. *B. evansiana* Andrews, 1811.

Diploclinium evansianum (Andrews) Lindl., Veg. Kingd., ed. 1 318, t. 220, 1846.

Knesebeckia discolor (R.Br.) Klotzsch, Abh. Königl. Akad. Wiss. zu Berlin, p. 164, 1854.

sinensis A.DC., Ann. Sci. Nat. Bot., sér. IV 11: 125, 1859.

martini H.Lév., Bull. Soc. Agric. Sarthe 39: 323, 1904.

bulbosa H.Lév., Feddes Repert. Sp. Nov. No. 131/133, 7: 21, 1909.

erubescens H.Lév., Feddes Repert. Sp. Nov. No. 131/133, 7: 21, 1909.

sinensis var. *haematoneura* Franch. ex Gagnepain, Bull. Mus. Hist. Nat. (Paris) 25: 283, 1919 pro. syn. *B. evansiana,* nom. inval. (Art. 34.1 (c)).

grandis conta. *evansiana* (Andrews) Irmsch., Mitt. Inst. Allg. Bot. Hamburg 10: 492, 1939.

grandis conta. *evansiana* var. *simsii* Irmsch., Mitt. Inst. Allg. Bot. Hamburg 10: 493, 1939.

grandis subsp. *evansiana* var. *simsii* (Irmsch.) Golding & Kareg. in L.B.Sm., Smithsonian Contr. Bot. 60: 174, 1986.

grandis conta. *sinensis* (A.DC.) Irmsch., Mitt. Inst. Allg. Bot. Hamburg 10: 494, pl. 13, 1939.

grandis subsp. *evansiana* (Andrews) F.A.Barkley & Golding, Sp. Begoniaceae, ed. 2, p. 48, 1974.

grandis subsp. *evansiana* var. *simsii* (Irmsch.) Golding & Kareg. in L.B.Sm., Smithsonian Contr. Bot. 60: 174, 1986.

grandis var. *simsii* (Irmsch.) F.A.Barkley & Golding, Sp. Begoniaceae, ed. 2, p. 48, 1974.

grandis subsp. *sinensis* (A.DC.) F.A.Barkley & Golding, Sp. Begoniaceae, ed. 2, p. 48, 1974.

grandis var. **unialata** Irmsch.; F.A.Barkley & Golding, Sp. Begoniaceae, ed. 2, p. 48, 1974.

grandis conta. *evansiana* var. *unialata* Irmsch., Mitt. Inst. Allg. Bot. Hamburg 10: 493, 1939.

grandis subsp. *evansiana* var. *unialata* Irmsch.; Golding & Kareg. in L.B.Sm. et al., Smithsonian Contr. Bot. 60: 174, 1986.

grandis var. **puberula** Irmsch., Mitt. Inst. Allg. Bot. Hamburg 10: 496, 1939.

grandis conta. *sinensis* var. *puberula* Irmsch., Mitt. Inst. Allg. Bot. Hamburg 10: 496, 1939.

grandis subsp. *sinensis* var. *puberula* Irmsch.; F.A.Barkley & Golding, Sp. Begoniaceae, ed. 2, p. 48, 1974.

grandis subsp. **holostyla** Irmsch. Mitt. Inst. Allg. Bot. Hamburg 10: 498, pl.s 14, 15, 1939; Golding & Kareg. in L.B.Sm. et al., Smithsonian Contr. Bot. 60: 174, 1986. **China**

sinensis sensu Hook.f., in Bot. Mag. Ser. 3 55, t. 7673, 1899, non A.DC., 1859.

yunnanensis sensu Gagnep., Fl. Indo-Chine 2(8): 1098, 1921, H.Lév., 1909.

grandis conta. reg. *holostyla* Irmsch., Mitt. Inst. Allg. Bot. Hamburg 10: 498, pl. 14, 15, 1939.

holostyla sensu F.A.Barkley & Golding, Sp. Begoniaceae, ed. 2, p. 48, 1974, non Irmsch., 1939.

gulinqingensis S.H.Huang & Shui, Acta Botanica Yunnan. 16(4): 334, fig. 2, 1994. **China**

Yunnan, Maguan Xian, Gulinqing, 1730 m, in wood, Dec. 1991, *Shui Yumin* B91 448 (holotype: YUNU).

guishanensis S.H.Huang et Shui, Acta Botanica Yunnan. 16(4): 336-337, fig. 4, 1994. **China**

Yunnan, Lunan Xian, Guishan, 1990 m, July 1991, *Shui Yumin* B91-651 (holotype: YUNU); ibidem, Aug. 1990, *Shui Yumin* B90-44 (paratype).

hymenocarpa C.Y.Wu, Acta Phytotax. Sin. 33(3): 256, 1995. **China**

Guangxi: Rongshui, Sanfang, Jiuwan Mt., 500-700 m, by streams in valley, July 1958, *S. Q. Chen* 16309 (holotype: KUN); ibidem, July 1958, *S. Q. Chen* 14804, 15749, 16499 (paratypes).

imitans Irmsch., Mitt. Inst. Allg. Bot. Hamburg 10: 511, 1939. **China**

Szetschwan, bei Tachienlu, 9000-13500 ft, Pratt 416 (holotype: K).

josephi A.DC., Ann. Sci. Nat. Bot., sér. IV 11: 126, 1859. **Himalayas**

picta sensu Wall., 1831, non Sm. 1805.

josephi var. *macrocarpa* A.DC., Prodr. 15(1): 314, 1864.

scutata sensu Wall., 1831, Num. List 3686A, nomen nudum, non Wall. ex A.DC., 1864.

josephi var. *minima* C.B.Clarke in J.D. Hooker, Fl. Brit. Ind. 2: 639, 1879.

labordei H.Lév., Bull. Soc. Agric. Sarthe 59: 323, 1904. **China**

harrowiana Diels, Notes Roy. Bot. Gard. Edinb. 5: 166, 1912.

polyantha H.Lév., Catalogue des plantes du Yun-nan: 17, 1915.

henryi × *sinensis?* Irmsch., Mitt. Inst. Allg. Bot. Hamburg 6: 356, 1927.

leptoptera H.Hara, J. Jap. Bot. 48(4): 98, pl. 1, 1973. **Nepal**

C. Nepal, Kalingchok, Thala - Tale Bisauna, 2500 m, 10.ix.1970, *Kanai, Chuma & Nagano* 4032 (holotype: TI).

adscendens sensu H.Hara, 1971, non C.B.Clarke, 1890.

lithophila C.Y.Wu, Acta Phytotax. Sin. 33(3): 257, 1995. **China**

Yunnan: Lunan, Shilin, 2000 m, on rocks, 26.viii.1956, *K. M. Feng* s.n. (holotype: KUN); ibidem, 1783 m, 6.xi.1990, *Y. M. Shui* 72 (paratype); ibidem, 1670 m, 6.x.1991, *Y. M. Shui* B91-650 (paratype); Eshan Mt., 1750 m, on rocks, 3.x.1958, *S. K. Wu* 206 (paratype); Yiliang, *Z. H. Yang*, 1800 m, on limestone cave at hillfoot, *B. Y. Qiu* 771073 (seedlings); Shiping, 1300 m, *A. Henry* 13347 (E, fide Irmsch. as *B. taliensis*).

malipoensis S.H.Huang et Shui, Acta Botanica Yunnan. 16(4): 333, fig. 1, 1994. **China**

Yunnan, Malipo Xian, Douchidian, 1300 m, June 1991, *Shui Yumin* B91-181 (holotype: YUNU).

minicarpa H.Hara, J. Jap. Bot. 47: 112, pl. 2, 1972. **Nepal**

Nepal, Dharan, ca. 630 m, 2.ix.1967, *Williams & Stainton* 8319 (holotype: BM); Morang Hills, 14.vii.1810, *Wallich* 3674 (paratype: K-W).

parviflora Buch.-Ham. ex Wall., Numer. List. 129, no. 3674, 1831, nomen nudum, non Poeppig & Endlicher, 1835.

wallichiana Steud., Nom. Bot., ed. 2, 1: 194, 1840, nomen nudum; J. Doorenbos, Begonian, 42: 213, 1975; H.Hara, J. Jap. Bot. 47: 112, 1972.

modestiflora sensu C.B.Clarke in J. D. Hooker, Fl. Brit. Ind. 2: 640, 1879, quoad pl. ex Nepal; H. Hara, J. Jap. Bot. 47: 112, 1972.

miranda Irmsch., Notes Roy. Bot. Gard. Edinburgh 21: 36, 1951. **China**

Yunnan, Ping-bien Hsein, Ma-ka-che, 1600 m, on mount. slope, place or rock, leaf twig white hairs, dominant, 13.xii.1939, *C. W. Wang* 83032 (holotype: KUN).

modestiflora Kurz, Flora, 54: 296, 1871; H. Hara, J. Jap. Bot. 47: 133, 1972. **Burma**

yunnanensis H.Lév., Repert. Spec. Nov. Regni Veg. 7: 20, 1909. **China**

yunnanensis var. *hypoleuca* H.Lév., Cat. pl. Yun-nan 17, 1915, nomen nudum; Golding & Karegeannes in L. B. Smith et al., Smithsonian Contr. Bot. 60: 251, 1986, nom. inval. **China**

sootepensis var. *thorelii* Gagnep., in Lecomte, Fl. Indo-Chine 2: 1104, 1921. **Laos**

lushaiensis C.E.C.Fisch., Bull. Misc. Inform. No. 7: 273, 1928. **India**

yunnanensis var. *thorelii* (Gagnep.) Golding & Kareg., Phytologia 54: 499, 1984. **Laos**

modestiflora var. **sootepensis** (Craib) Z. Badcock comb. nov.

sootepensis Craib, Kew Bull. Misc. Infor. 58, 1911.

yunnanensis var. *sootepensis* Craib, Aberdeen Univ. Stud. 47: 96, 1912 **Thailand**

morifolia T.T.Yu, Bull. Fan. Mem. Inst. Biol., n.s. 1: 119, 1948. **China**

SE Yunnan, Si-chou-hsien, Fardoc, 1300 m., forest floor, moist situation, 4.xii.1939, *C. W. Wang* 85333. (holotype: KUN).

muliensis T.T.Yu, Bull. Fan. Mem. Inst. Biol., n.s. 1: 119, 1948. **China**

S. Sikang, Muli, Woosi, 2600 m., side of mt. stream, grassland, herb with tubers, 19.viii.1939, *T. T. Yu* 14024 (holotype: KUN); NW Yunnan, E. Chungtien, on the way to Lochi-ho, 2200 m., moist shady rocks, 20.viii.1939, *K. M. Feng* 2715 (paratype).

pedunculosa Wall., Pl. Asiat. Rar. 1: 82, pl. 97, 1830. **India**

picta Sm., Exot. Bot. 2: 81, pl. 101, 1805. **Himalayas**

hirta Wall. mss. ex W. J. Hooker, Exotic Flora. 2:89, 1825, pro syn.
picta Sm., 1807 (NB cited as 1807 by Hooker and not 1805).
echinata Royle, Ill. bot. Himal. Mts. 313, t. 80: fig. 1, 1839.
erosa Wall. ex C.B. Clarke in J. D. Hooker, Fl. Brit. Ind. 2: 638, 1879, non Blume, 1827; Hara in Enum. Nep. 2:182, 1979.
rex auct. non Putz., Liv. Him. Flow. t. 183, 1964; Hara in Enum. Nep. 2:182, 1979.

pingbianensis C.Y.Wu, Acta Phytotax. Sin. 33(3): 258, 1995. **China**
Yunnan, Pingbian, 1400m, in woods, 30.viii.1934, *H. T. Tsai* 61724 (holotype: KUN); same locality, 1500 m, by stream, 15.vii.1934, *H. T. Tsai* 62671 (paratypes: KUN, A); Malipo, 1000-1500 m, under evergreen forests, 25.xii.1934, *Vegetation group of Kunming Institute of Botany* 01-137 (paratype), "*pingbienensis*".

pingbianensis var. **angustior** C.Y.Wu, Acta Phytotax. Sin. 33(3): 259, 1995 "*pingbienensis* var. *angustior*". **Vietnam**
Vietnam: Laoke, Chapa, 240-1995 m by stream under forests, 10.xii.1964, *Sino-Vietnam Exped.* 295 (holotype: KUN).

rhodophylla C.Y.Wu, Acta Phytotax. Sin. 33(3): 260, 1995. **China**
Yunnan, Lunan, Changhu, 1800-2000 m, in mixed forests of limestone hills, 2.viii.1984, *Sino-American Exped.* 1577 (holotype: KUN; isotype: SA); ibidem, 1960 m, 4.xi.1990, *Y. M. Shui Lunan* 44 (paratype); ibidem, Haiyi, 1900 m, 7.x.1991, *Y. M. Shui* B91-651 (paratype).

rongjiangensis T.C.Ku, Acta Phytotax. Sin. 33(3): 279, 1995. **China**
Guizhou: Rongjiang, Yueliang Mt., by streams on slopes, 3.viii.1958, *South Guizhou Exped.* 3165 (holotype: PE).

rotundilimba S.H.Huang & Shui, Acta Botanica Yunnan. 16(4): 335, fig. 3, 1994. **China**

Yunnan, Pingbian Xian, Timi, 1600-1800 m, April 1959, *Exped. Univ. Yunnan* 59-8 (holotype: YUNU); ibid., July 1991, *Shui Yumin* B91 470 (paratype).

ruboides C.M.Hu ex C.Y.Wu & T.C.Ku, Acta Phytotax. Sin. 33(3): 262, 1995. **China**

Yunnan: Pingbian, Yaoshan Mt., Chongtou, Dazhupeng, 1300 m, in sparse woods, 10.iv.1954, *P. Y. Mao* 3761 (holotype: KUN; isotype PE); same locality, 15.iv.1953, *P. Y. Mao* 2541 (paratype); same locality, 18.iii.1954, *P. Y. Mao* 3467 (paratype); Jinping, 2200 m, 1956, *Sino-Russian Exped.* 1165 (paratype).

satrapis C.B.Clarke in J. D. Hooker, Fl. Brit. Ind. 2: 638, 1879. **India**

sino-vietnamica C.Y.Wu, Acta Phytotax. Sin. 35(1): 50, fig. 30, 1997 "sino-veitnamica". **China**

Guangxi, Dongxing, Tansan, 230 m, on slopes, under forests, 17.viii.1975, *X. P. Fang et D. Fang* 76603 (holotype: GXMI); same locality, by stream, 12.x.1976, *Exped. Naqin.* 432 (paratype); Guiping, Zijing, Mt. Qilin, 9.v.1977, *Exped. Guiping* 8-1582 (paratype).

summoglabra T.T.Yu, Bull. Fan. Mem. Inst. Biol., n.s. 1: 117, 1948. **China**

SE Yunnan, Ping-pien, Shu-pan-po, alt. 1400 m., on rock surface, moist place, 2-5 in. high, 24.ix.1939, *C. W. Wang* 82099. (holotype: KUN); same locality, seeds collected, 2.xii.1939, *C. W. Wang* 82910 (paratype).

surculigera Kurz, Flora 54: 296, 1871. **Burma**

"Haufig auf feuchten Sandsteinfelsen, die mit Moos bedeckt sind, in gemischten und immergrunen Waldern des Akyab. Districts, Arracan - Bluthen und Fruchte im Oktober", *Kurz* s.n. (holotype: K).

tribensis C.R.Rao, J. Bombay Nat. Hist. Soc. 65: 724, pl., "1968," 1969. **Nepal**

East Nepal, Sunsari District, from Barakshetra to Tribeni, ±130 m, 6.vii.1963, Rao 342A (holotype: BLAT); Rao 342B (isotype: HBG missing); Rao 832A, 832B (paratypes: BLAT).

wenshanensis C.M.Hu ex C.Y.Wu & T.C.Ku, Acta Phytotax. Sin. 33(3): 262, 1995. **China**

Yunnan, Wenshan Mt., 2200 m, in mixed forests, 17.viii.1947, *K. M. Feng* 11323 (holotype: PE; isotype: KUN); Laojun Mt., 1800-2200 m, in mixed forests, 12.viii.1947, *K. M. Feng* 11106 (paratype); Funing, Lida, Ligong, 1290 m, in moist evergreen forests, 12.x.1964, *Q. A. Wu* et al. 9594 (paratype); Ligong, Houlong Mt., 1410 m, by streams under forests, 29.x.1965, *Wenshan Exped.* 65-177 (paratype).

wilsonii Gagnep., Bull. Mus. Natl. Hist. Nat. (Paris) 25:279, 1919. **China**

xingyiensis T.C.Ku, Acta Phytotax. Sin. 33(3): 263, 1995. **China**

Guizhou, Xingyi, Yangping, Bajiaotang, 1100 m, on rocks in valley, 7.viii.1959, *Anshun Exped.* 748 (holotype, PE).

xinyiensis T.C.Ku, Acta Phytotax. Sin. 33(3): 263, 1995. **China**

Guangdong: Xinyi, by stream in valley, 21.iii.1931, *Z. Huang* 31748 (holotype, PE).

xishuiensis T.C.Ku, Acta Phytotax. Sin. 33(3): 264, 1995. **China**

Guizhou, Xishui, Changkan, 480 m, on shady and wet rocks, 28.v.1965, *collector unknown* 311 (holotype: HGAS).

yui Irmsch., Notes Roy. Bot. Gard. Edinburgh 21: 36, 1951, "yüii". **China**

Yunnan, Mien-ning, Po-shang, 2500 m., under forest, on rock surface, 8.x.1938 *T. T. Yu* 17945 (holotype: KUN).

4.4 TAXA WHICH SHOULD BE INCLUDED IN ANY FUTURE INVESTIGATION TO DELIMIT SECTION *DIPLOCLINIUM*

Together with the taxa already listed as belonging to section *Diploclinium* in Barkley & Golding (1974), species listed as section *Trilobaria* A.DC. also require investigation.

During the course of this study *B. rubella* Buch.-Ham. ex D.Don. (=*B. scutata* Wall. ex A.DC.) was found to be very closely related to *B. josephi* differing only by cordate leaves (not peltate leaves) and three tepals in the female flower (not five). The type of section *Trilobaria*, *B. dioica* Buch.-Ham. ex D.Don, and *B. laguensis* Elmer (sect. *Diploclinium*) are distinguished by their very large, spindle shaped, seeds, c. 0.9 mm (Bouman, pers. comm.). This would suggest that section *Trilobaria*, as currently delimited, is not monophyletic.

From the evidence already presented in this thesis, e.g. chapters 2, paragraph 2.4.7 and my experiences of looking through Asian collections of *Begonia* in herbaria in Great Britain, Leiden and Paris, it is highly improbable that the species now included in section *Diploclinium* form a cohesive monophyletic group. The species listed here need to be included in any study to delimit this group. It is my opinion that those species listed below, from Thailand and those from the Philippines, may form the core of two separate groups. Delimitation of these groups was beyond the scope of this thesis and would require a considerable amount of work.

Listed below are the species included in sections *Diploclinium* and *Trilobaria* in Barkley & Golding (1974) and, as far as possible, subsequent authors. Synonyms are in italics and follow Smith *et al.* (1986).

4.4.1 TAXA PREVIOUSLY INCLUDED IN *DIPLOCLINIUM SENSU* F.A.BARKLEY & GOLDING, 1974 AND *TRILOBARIA SENSU* F.A.BARKLEY & GOLDING, 1974

acaulis Merr. & Perry, J. Arnold Arbor. 24: 43, pl. 1,1-q, 1943. **New Guinea**

aceroides Irmsch., Bot. Jahrb. Syst. 76: 100, 1953. **Thailand**

burkillii Irmsch., Mitt. Inst. Allg. Bot. Hamburg 8:116, 1929, non Dunn, 1920; Irmscher, Bot. Jahrb. Syst. 76: 100, 1953.

acuminatissima Merr., Philipp. J. Sci. 6: 395, "1911," 1912. **Philippines**

camiguinensis Elmer, Leafl. Philipp. Bot. 7: 2553, 1915; Merrill, Enum. Philipp. Fl. pl. 119, 1923.

aequata A.Gray, U.S. Expl. Exped. Phan. 15: 658, 1854; Merrill, Philipp. J. Sci. 3: 84, pl. 4, 1908. **Philippines**

alba Merr., Philipp. J. Sci. 10: 45, 1915. **Philippines**

alvarezii Merr., Philipp. J. Sci. 6: 405, "1911," 1912. **Philippines**

anisoptera Merr., Philipp. J. Sci. 6: 398, "1911," 1912. **Philippines**

areolata Miq., Pl. Jungh. 4: 417, "1855", 1857. **Java**

Diploclinium areolatum Miq., Fl. Ned. Ind. 1.1: 689, 1856; A.DC., Prodr. 15(1): 397, 1864.

papillosa Reinwardt in Koord., Exkurs.-Fl. Java 2: 650, 1912, non Graham, 1828, non Lindl., 1841, pro syn. *areolata* Miquel, 1857.

arnottiana (Wight) A.DC., Prodr. 15(1): 322, 1864; C. B. Clarke in J. D. Hooker, Fl. Brit. Ind. 2: 641, 1879; Smith & Wasshausen, Phytologia 52: 441, 1983, nomen illegitimum; non *cordifolia* Thwaites, 1859. **India**

Diploclinium arnottianum Wight, Icon. pl. Ind. orient. 1: 9, 3, pl. 1815, 1852; A.DC., Prodr. 15(1): 322, 1864.

bartlettiana Merr. & Perry, J. Arnold Arbor. 29: 160, 1948. **New Guinea**

bifolia Ridl., J. Fed. Malay States Mus. 8(4): 40, 1917. **Sumatra**

biliranensis Merr., Philipp. J. Sci. 10: 46, 1915. **Philippines**

brassii Merr. & Perry, J. Arnold Arbor. 24: 43, pl.2a-f, 1943. **New Guinea**

carnosa (Teijsm. & Binn.) Teijsm. & Binn., Epim. Lugd. Bat. 4. 1863. **Moluccas**

Diploclinium carnosum Teijsm. & Binn., Tijdschr. Ned.-Indië 25: 420, 1863.

castilloi Merr., Philipp. J. Sci. 13: 38, 1918. **Philippines**

cavaleriei H.Lév., Repert. Spec. Nov. Regni Veg. 7: 20, 1909. **China**

esquirolii Lév., Bull. Acad. Int. Géogr. Bot. 22: 228, 1912; Irmscher, Mitt. Allg. Bot. Hamburg 10: 512, 1939.

cavaleriei var. **pinfaensis** H.Lév., Repert. Spec. Nov. Regni Veg. 7: 20, 1909. **China**

collisiae Merr., Philipp. J. Sci. 14: 424, 1919. **Philippines**

colorata Warb. in Perkins, Fragm. Fl. Philipp. 51, 1904. **Philippines**

copelandii Merr., Philipp. J. Sci. 6: 401, "1911," 1912. **Philippines**

cordifolia (Wight) Thwaites, Enum. Pl. Zeyl. 129, 1859. **Ceylon**

Diploclinium cordifolium Wight, Icon. pl. Ind. orient. 1: 9, 3, pl. 1816, 1852; Thwaites, Enum. Pl. Zeyl. 129, 1859.

coronensis Merr., Philipp. J. Sci. 26: 480, 1925. **Philippines**

dioica Buch.-Ham. ex D.Don., Prodr. Fl. Nepal. 223, 1825. **Himalayas**

tenella, D. Don, Prodr. Fl. Nepal. 223, 1825; H. Hara in H. Ohashi, Fl. E. Himal. 3: 85, 1975.

amoena, Wall., Numer. List 129, no. 3682, 1831, *nomen nudum*; Wall. ex A.DC., Prodr. 15(1): 327, 1864; H. Hara in H. Ohashi, Fl. E. Himal. 3: 83, pl. 5d, 1975.

discreta Craib, Bull. Misc. Inform. 410, 1930. **Thailand**

edanoi Merr., Philipp. J. Sci. 13: 314, 1918, "edanoii". **Philippines**

elmeri Merr., Philipp. J. Sci. 13: 39, 1918. **Philippines**

peltata Elmer, Leafl. Philipp. Bot. 7: 2556, 1915, non Otto & A.Dietr., 1841; Merrill, Philipp. J. Sci. 13(1): 39, 1918.

fenicis Merr., Philipp. J. Sci. 3: 421, 1908. **Philippines**

kotoensis Hayata, J. Coll. Sci. Imp. Univ. Tokyo 30: 124, 1911; Liu & Lai, Fl. Taiwan, ed. 1 3: 793, 1977.

festiva Craib, Bull. Misc. Inform. 411, 1930. **Thailand**

flacca Irmsch., Webbia 9: 486, pl. 4, 1953. **Celebes**

flexicaulis Ridl., Trans. Linn. Soc. London Bot. sér. II 9: 59, 1916. **New Guinea**

fruticella Ridl., Trans. Linn. Soc. London Bot. sér. II 9: 60, 1916. **New Guinea**

garrettii Craib, Bull. Misc. Inform. 411, 1930. **Thailand**

gitingensis Elmer, Leafl. Philipp. Bot. 2: 738, 1910. **Philippines**

gracilipes Merr., Philipp. J. Sci. 6: 405, "1911," 1912. **Philippines**

grandipetala Irmsch., Bot. Jahrb. Syst. 50: 377, 1913. **Celebes**

harmandii Gagnep., Bull, Mus. Natl. Hist. Nat. (Paris) 25: 200, 1919. **S. Vietnam**

hasskarliana (Miq.) A.DC., Prodr. 15(1): 329, 1864. **Sumatra**

Diploclinium hasskarlianum Miq., Fl. Ned. Ind. 1.1: 1091, 1858; A.DC. Prodr. 15(1): 329, 1864.

hasskarliana Miq., in herb. Teysm., Fl. Ned. Ind. 1: 1091, 1858, pro syn. *Diploclinium hasskarlianum* Miq., 1858; A.DC., Prodr. 15(1): 329, 1864.

hernandioides Merr., Philipp. J. Sci. 6: 392, "1911," 1912. **Philippines**

heteroclinis Miq. ex Koord., Meded. Lands Plantentuin 19: 484, 1898. **Celebes**

holosericea (Teijsm. & Binn.) Teijsm. & Binn., Epim. Lugd. Bat. 5, 1863. **Mollucans**

Diploclinium holosericeum Teijsm. & Binn., Tijdschr. Ned.-Indië 25: 421, 1863.

horsfieldii Miq. Fl. Ned. Ind. 1.1: 691, 1856, pro syn. *Diploclinium horsfieldii* Miq., 1856. **Sumatra**

Diploclinium horsfieldii Miq., Fl. Ned. Ind. 1.1: 691, 1856; Miq. ex A.DC., Prodr. 15(1): 397, 1864.

incondita Craib, Bull. Misc. Inform. 412, 1930. **Thailand**

ionophylla Irmsch., Bot. Jahrb. Syst. 50: 378, 1913. **Sumatra**

isabelensis Quisumb. & Merr., Philipp. J. Sci. 37: 173, 1928. **Philippines**

kaniensis Irmsch., Bot. Jahrb. Syst. 50: 373, 1913. **New Guinea**

klemmei Merr., Philipp. J. Sci. 6: 402, "1911", 1912. **Philippines**

lagunensis Elmer, Leafl. Philipp. Bot. 2: 735, 1910. **Philippines**

lancilimba Merr., Philipp. J. Sci. 14: 424, 1919. **Philippines**

longinoda Merr., Philipp. J. Sci. 6: 397, "1911," 1912. **Philippines**

longiscapa Warb. in Perkins, Fragm. Fl. Philipp. 52, 1904. **Philippines**

longovillosa A.DC., Ann. Sci. Nat. Bot. sér. IV 11: 130, 1859. **Philippines**

luzonensis Warb. in Perkins, Fragm. Flor. Philipp. 52, 1904. **Philippines**

bakeri Elmer, Leafl. Philipp. Bot. 10: 3706, 1939, non C.DC., 1908; Smith & Wasshausen, Phytologia 52: 441, 1983. **Philippines**

manillensis A.DC., Ann. Sc. Nat. sér. IV 11: 129, 1859. **Philippines**

mindorensis Merr., Philipp. J. Sci. 6: 396, "1911," 1912. **Philippines**

sordidissima Elmer, Leafl. Philipp. Bot. 7: 2557, 1915; Merrill, Enum. Philipp. Fl. Pl. 3: 125, 1923.

minjemensis Irmsch., Bot. Jahrb. Syst. 50: 375, pl. 4, 1913. **New Guinea**

moulmeinensis C.B.Clarke in J.D.Hooker, Fl. Brit. Ind. 2: 643, 1879. **Burma**

muricata Blume, Catalogus 103, 1823; Enum. Pl. Javae 95, 1827. **Indonesia**

Empetrum acetosum f. *album* Rumph., Herb. Amboin. 5: 457, pl. 169: fig. 2, 1747, nom. inval.; Merrill, Interp. Herb. Amboin. 379, 1917; Smith & Wasshausen, Phytologia 54: 471, 1984.

Empetrum acetosum f. *rubrum* Rumph., Herb. Amboinese 5: 457, 1747, nom. inval.; Hasskarl, Neu Schuss. Rumph. 146, 1866; Merrill, Interp. Herb Amboin. 379, 1917; Smith & Wasshausen, Phytologia 54: 471, 1984.

tuberosa Lam., Encycl. 1: 393, 1785, nomen validum sed illegitimum non; Merrill, Interp. Herb. Ambion. 379, 1917; Backer & Van den Brink, Fl. Java 1: 309, 1964; Smith & Wasshausen, Phytologia 52: 446, 1983.

rubra Blume, Enum. Pl. Javae 1: 96, 1827; Miquel, Fl. Ned. Ind. 1: 689, 1856; Hasskarl, Hort. Bogor. Descr. 349, 1858; Neu Schuss. Rumph. 146, 1866; Merrill, Interp. Herb. Amboin. 379, 1917.

saxatilis Blume, Enum. Pl. Javae 1: 95, 1827; Backer & Van den Brink, Fl. Java 1: 309, 1964.

Diploclinium tuberosum Miq., Fl. Ned. Ind. 1.1: 685, 1856; A.DC., Prodr. 15(1): 323, 1864; Merrill, Interp. Herb. Amboin. 379, 1917; Smith & Wasshausen, Phytologia 52: 446, 1983.

Diploclinium rubrum (Blume) Miq., Fl. Ned. Ind. 1.1: 689, 1856; Hasskarl, Neu Schuss. Rumph. 146, 1866; Merrill, Interp. Herb. Amboin. 379, 1917.

Diploclinium saxatile (Blume) Miq., Fl. Ned. Ind. 1.1: 686, 1856; A.DC., Prodr. 15(1): 351, 1864; Backer & Van den Brink, Fl. Java 1: 309, 1964.

Sphenanthera robusta Hassk. var. *rubra* Hassk., Hort. Bogor. Descr. 349, 1858; A.DC., Prodr. 15(1): 275, 1864; Smith & Wasshausen, Phytologia 54: 472, 1984.

Casparya robusta A.DC. var. *rubra* A.DC., Prodr. 15(1): 275, 1864; Smith & Wasshausen, Phytologia 54: 471, 1984.

robusta Blume var. *rubra* (A.DC.) Warb., in Engler & Prantl, Nat. Pflanzenfam. 3(6A): 146, 1894; Smith & Wasshausen, Phytologia 54: 471, 1984.

forbesii Vuijck ex Koord., Exkurs.-Fl. Java 2: 649, 1912, pro syn. *muricata* Blume, 1823.

glabra Vuijck ex Koord., Exkurs.-Fl. Java 2: 649, 1912, pro syn. *vuijckii* Koord., 1912.

rumphii Vuijck ex Koord., Exkurs.-Fl. Java 2: 649, 1912, pro syn. *muricata* Blume, 1823.

murina Craib, Gard. Chron., sér. III 83: 66, 1928. **Thailand**

nigritarum Steud., Nom. Bot. 1: 104, 1821. **Philippines**

Acetosa nigritarum Kamel, in J. Ray, Herb. Philipp. 3(app.): 14, 1704, nom. inval.; Steudel, Nom. Bot. 1: 104, 1821.

capensis Blanco, Fl. Filip. 724, 1837; Naves, Fl. Filip., ed. 3 3: 127, pl. 413, 1879; Merrill, Philipp. J. Sci. 6: 393, 1911.

rhombicarpa A.DC., Ann. Sci. Nat. Bot., sér. IV 11: 129, 1859; Merrill, Philipp. J. Sci. 6: 394, 1911.

rhombicarpa var. *lobbii* A.DC., Prodr. 15(1): 323, 1864; Merrill, Philipp. J. Sci. 6: 395, 1911.

merrillii Warb. in Perkins, Fragm. Flor. Philipp. 53, 1904; Merrill, Philipp. J. Sci. 6: 394, "1911,", 1912.

notata Craib, Gard. Chron., sér. III 83: 66, 1928. **Thailand**

obtusifolia Merr., Philipp. J. Sci. 14: 425, 1919. **Philippines**

oligandra Merr. & Perry, J. Arnold. Arbor. 24: 44, pl. 2.g-k, 1943. **New Guinea**

orbiculata Jack, Malayan Misc. 2(7): 9, 1822. **Sumatra**

Diploclinium orbiculatum (Jack) Miq., Fl. Ned. Ind. 1.1: 686, 1856; A.DC., Prodr. 15(1): 398, 1864.

ovatifolia A.DC., Ann. Sci. Nat. Bot. sér IV 11: 132, 1859. **Himalaya**

subovata Wallich, Numer. List. 129, no. 3683, 1831, nomen nudum; Wall. ex C.B. Clarke in J. D. Hooker, Fl. Brit. Ind. 2: 642, 1879; J. Golding, Phytologia 40: 15, 1978.

ovatifolia var. *cretacea* C.B.Clarke in J.D. Hooker, Fl. Brit. Ind. 2: 643, 1879.

parva Merr., Philipp. J. Sci. 6: 402, "1911," 1912. **Philippines**

peltatifolia Li, J. Arnold Arbor. 25: 209, 1944. **China**

pentaphragmifolia Ridl., Trans. Linn. Soc. London Bot. 9: 59, 1916. **New Guinea**

pierrei Gagnep., Bull. Mus. Natl. Hist. Nat. (Paris) 25: 276, pl., 1919. **Indo-China**

pilosa Jack, Malayan Misc. 2(7): 13, 1822. **Sumatra**

Diploclinium pilosum (Jack) Miq., Fl. Ned. Ind. 1.1: 688, 1856; A.DC., Prodr. 15(1): 398, 1864.

pinamalayensis Merr., Philipp. J. Sci. 26: 479, 1925. **Philippines**

putii Craib, Gard. Chron. sér. III 83: 67, 1928. **Thailand**

rubrifolia Merr., Philipp. J. Sci. 14: 426, 1919. **Philippines**

rufipila Merr., Philipp. J. Sci. 6: 393, "1911," 1912. **Philippines**

sarmentosa L.B.Sm. & Wassh., Phytologia 52: 443, 1983. **Philippines**

elegans Elmer, Leafl. Philipp. Bot. 7: 2554, 1915, non Humb., Bonpl. & Kunth, 1825.

saxifragifolia Craib, Bull. Misc. Inform. 416, 1930. **Thailand**

serpens Merr., Philipp. J. Sci. 14: 427, 1919. **Philippines**

soluta Craib, Bull. Misc. Inform. 418, 1930. **Thailand.**

subcyclophilla Irmsch., Bot. Jahrb. Syst. 50: 374, 1913. **New Guinea**

subnummulariifolia Merr., Philipp. J. Sci. 29: 403, 1926, "*subnummularifolia*". **Borneo**

suborbiculata Merr., Philipp. J. Sci. 6: 398, "1911," 1912. **Philippines**

subperfoliata Parish ex Kurz, J. Asiat. Soc. Bengal 42(2): 81, 1873. **Burma**

tayabensis Merr., Philipp. J. Sci. 13: 38, 1918. **Philippines**

trichochila Warb. in Perkins, Fragm. Flor. Philipp. 53, 1904. **Philippines**

vanoverberghii Merr., Philipp. J. Sci. 6: 403, "1911," 1912. **Philippines**

vitiensis A.C.Smith, Bernice P. Bishop Mus. Bull. 141: 99, pl. 52, 1936. **Fiji**

woodii Merr., Philipp. J. Sci. 26: 478., 1925. **Philippines**

zamboangensis Merr., Philipp. J. Sci. 26: 481, 1925. **Philippines**

4.5 SPECIES DESCRIPTIONS OF TAXA CONTRIBUTING TOWARDS A REVISION OF *BEGONIA* L. SECTION *DIPLOCLINIUM* LINDL.

There are about 130 species in the temporarily enlarged section, *Diploclinium* Lindl., 44 of which were erroneously placed in section *Knesebeckia* (Klotzsch) A.DC. Included below are 11 species descriptions. These have been included to improve the knowledge of these species and with the inclusion of *B. grandis*, the type of section *Diploclinium*, form the basis for any future revision of the section. The taxa do not form a group of most closely related taxa as they were chosen for revision before much knowledge of the section had been gained; however, they are the oldest known species in the section

(except *B. surculigera* Kurz) with species descriptions concomitant to their age, i.e. (in these cases) depauperate. The species treated represent the geographical and the majority of the morphological diversity in *Knesebeckia*, as previously circumscribed.

4.5.1 CONVENTIONS AND TERMINOLOGY IN DESCRIPTIONS

The descriptions follow the monographic style of those descriptions published by the Dutch Wageningen group (e.g. Sosef, 1994) and the citation of specimens follows the instructions for authors from the *Edinburgh Journal of Botany*. The reader is referred to chapter 2, paragraphs 2.2.2.1 - 2.2.2.7 for a detailed discussion and explanations of the terminology involved in the description of the morphology of *Begonia*.

FIG. 4.1 MAP TO SHOW THE DISTRIBUTION OF *B. ADSCENDENS, B. ASPERIFOLIA, B. FIMBRISTIPULA, B. JOSEPHI* AND *B. LABORDEI*

4.5.2 *B. ADSCENDENS* C.B.CLARKE "*ASCENDENS*"

PLACE OF PUBLICATION: J. Linn. Soc. 25: 26, t.13, 1890

TYPE: India, (Assam), Nagaland, Jakpho, Naga Hills, 8500 ft, 25.x.1885, *C. B. Clarke* 41240 (lectotype designated here: K!); same details, *C. B. Clarke* 41247 (syntype: K!).

NOTE: This species was published under the name "*B. adscendens*", but the accompanying illustration and both the type specimens were labelled "*B. ascendens*" by C. B. Clarke. Although this may be treated as a correctable typographical error (Art. 60.1, ICBN), the error occurs in the first syllable and may therefore be left uncorrected. I have not corrected this error as all publications have followed the orthography, "*B. adscendens*".

DESCRIPTION: **Acaulescent,** succulent herb up to c. 50 cm tall (base of plant not observed). **Bulbils** not observed. **Stipules** not observed. **Petiole** 5-20 cm, hirsute, glandular hairs up to 1 mm; **leaf blade** leathery, upper surface ± glabrous (to hispid), lower surface veins hirsute, margin sparsely fimbriate, slightly asymmetric, very broadly ovate to subspherical, 8.5-16 × 8-18 cm, leaf base unequally cordate, lobes up to 5 cm deep, not overlapping, apex acuminate, margin shallowly serrulate to denticulate, palmate-pinnate veination of 6-9 main veins, 4-5 veins reaching margin in small lobe, 5-6 in large lobe. **Inflorescence** a terminal, ± symmetrical dichasial cyme, 1-8 flowered, peduncle up to 22 cm; **bracts** deciduous, at first branching point linear-ovate, 4-6 × 2 mm, apex rounded to acute, margin entire, at later branching points triangular-ovate, 1.8 × 1.0 mm, apex acute, margin entire. **Male flowers**: not observed. **Female flowers** [not observed except for 3 tepals persisting on one fruit capsule]; **pedicels** 3-7 mm, elongating in fruit; **tepals** ?3, outer pair subequal, ovate, 7-7.8 × 3.8-4.2 mm, apex acute, margin entire; inner tepal obovate, 4.2 × 3 mm, apex rounded, margin entire; **ovary** not observed (when young), 3-locular, placentae axile, bilamellate, bearing numerous, minute ovules on both sides; **styles** 3, persistent, briefly fused at base for c.

0.4 mm, whole style c. 2 mm, reniform, branches c. 0.2 mm, a continuous papillose stigmatic band encircling tops of styles. **Capsule** becoming scarious, 25-32 × 9-18 mm, main body obovoid-cordate, 8-15 × 5.2-9 mm, wings 3, 1 much longer, up to 27 mm, upper margin straight to concave, ascending slightly or up to 90°, lower margin straight to convexly curved, c. 45 mm, tip acute to rounded, 2-4 mm wide distally, wings exceeding the capsule c. 1 mm distally, c. 2 mm proximally; dehiscence at margins of capsule body.

DISTRIBUTION: India, Assam - Sirhoi, Jakpho mountain; West Central Burma. See fig. 4.1.

ECOLOGY & BIOLOGY: Found growing epiphytically on big moss-clad tree trunks in dense jungle, on a northern slope at 2500 m in Sirhoi (*F. Kingdon-Ward* 18245), on southern facing cliffs at 2500 m on Mt. Victoria in West Central Burma (*F. Kingdon-Ward* 22822) and on vertical rock faces at 2800 m in *Rhododendron* and deciduous tree forest (*Acer* sp.) in a north-east gulley in Kachin State, Burma (*F. Kingdon-Ward* 21489). This species appears to be deciduous during the winter months. (The location of Sirhoi was identified using Kingdon-Ward, 1952).

NOTE: The rhizome has been described as small and spherical (*F. Kingdon-Ward* 22822, BM).

DISCUSSION: The distribution of this species is an interesting disjunction. There are several endemic species of plants (and birds) only on Mt. Victoria and it is the southern limit of several other more northerly species (like *B. adscendens*) (R. Mill, pers. comm.).

ADDITIONAL SPECIMENS EXAMINED: INDIA / BURMA: Sirhoi, 8000 ft, 23.x.48, *F. Kingdon-Ward* 18245 (BM); **BURMA:** (West Central), Mt. Victoria, 8000 ft, 5.xi.56, *F. Kingdon-Ward* 22822 (BM); Kachin State, North Triangle (Tama Bum), 9250 ft, 20.x.53, *F. Kingdon-Ward* 21489 (BM).

4.5.3 *B. ASPERIFOLIA* IRMSCH.

PLACE OF PUBLICATION: Mitt. Inst. Allg. Bot. Hamburg 6: 359 (1927); emend. Irmscher in Handel-Mazzetti (ed.), Symbolae Sinicae 7:389 (1931)

TYPE: China, NW Yunnan, in pluvii silvis mixtis temperatis vallis Doyon lumba ad fluvium Lu-djiang (Salween), ca. 28° 2' N, 2600-3000 m, fl. 1.viii.1916, fr. 24.ix.1915, (H. F. v. Handel-Mazzetti Diar. Nos. 1547, 1800), *Handel-Mazzetti Iter Sinense 1914-18* no. 9599 (lectotype designated by Irmscher in Handel-Mazzetti, 1931: WU!; isolectotype: WU!); same details, *Handel-Mazzetti* (Diar. No.s 1547, 1804), 9599 (isolectotype: B!); in pluvii silvis mixtis temperatis supra vicum Bahan (Pehalo) ad fluvium Lu-djiang (Salween), 27° 58' N, ca. 2700 m, 23.viii.1916, *Handel-Mazzetti* (Diar. Nr. 1858) 9939 (syntype: E; isosyntype: WU!).

DESCRIPTION: Acaulescent - occasionally caulescent, moliniform rhizomatous herb up to 65 cm tall. **Bulbils** not observed. **Stem** ± erect, 6-15 mm diam.; internodes occasionally up to 15 cm; **stipules** caducous, ovate-triangular, 6.4 × 2.5 mm, apex acute, margin entire. **Petiole** (2.2-)6.5-23(-32.5) cm, mostly glabrous, becoming hirsute towards apex (sparsely woolly in var. *tomentosa*), hairs occasionally bifid; **leaf blade** purplish green; upper leaf surface sparsely (- densely) tomentose, lower leaf surface ± glabrous - tomentose, especially on veins, slightly asymmetrical, borne at up to 90° to petiole, broadly ovate - subrotund, (5.5-)15-32 × (3-)11.5-24 cm, leaf base ± equally cordate, lobes (2-)3-5(-6.5) cm deep, sometimes overlapping, apex acuminate, margin shallowly lobed at vein endings, the lobes with acuminate apices, dentate - denticulate, occasionally serrate-serrulate, venation palmate-pinnate of 4-5 main veins, c. 5 veins reaching margin in each half. **Inflorescence** a terminal asymmetric dichasial cyme, c. 7 flowered, usually bisexual, male flowers usually maturing first; **bracts** early deciduous, glabrous, at first branching point broadly obovate, 10-14 × 7-11 mm, apex rounded - obtuse, margin entire, at later branching points ovate, 4-6 × 2-5 mm, apex rounded - acute, margin entire. **Male flowers: pedicels** 15-25 mm; **tepals** 4, white or pink, outer

pair (sepals) oblong-ovate to very broadly obovate, 8-13 × 7-12 mm, apex rounded, margin entire; inner pair (petals), obovate to broadly obovate, 4.2-9 × 3-6 mm, apex rounded, margin entire; **stamens** 36-44, androecium obovoid to subglobose, symmetrical, filaments fused basally into a column, 0.5-1.8 mm, the free filaments arising from upper part of the column, 0.6-1.0 mm, anthers ellipsoid-obovoid 0.8-1.2 × 0.4-0.6 mm, connective not extended, dehiscing through slits eventually down entire length of pollen sacs. **Female flowers: pedicels** c. 25 mm, elongating in fruit; **tepals** 5, white or pink, imbricate, 3 subequal, obovate, 7.2-11 × 6-9 mm, apex obtuse, margin entire; 2 subequal, narrowly oblong-obovate, 4-7 × 2-4 mm, apex acute to obtuse, margin entire; **ovary** obovoid, 8.5-9.5 × 5.6 mm, 3 wings, triangular, 1 longer, extending upwards, 2 rib-like, 3-locular, placentae axile, bilamellate, bearing numerous minute ovules on both sides; **styles** 3, persistent, ± free, united at base for c. 0.1-0.2 mm, whole style c. (1.4-)2.8-3.2 mm, reniform, becoming lunate when mature, branches 0.6-1.2 mm, a continuous papillose stigmatic band encircling top of styles. **Capsule** red, becoming scarious, 17-22 × 10-13 mm, main body obovoid (to obovoid-ellipsoid), 6-8.8 × 4.2 mm; wings 3, triangular, 1 longer, 14-18 mm, upper margin ± horizontal or ascending up to 45°, slightly repand, lower margin ± straight to slightly convex c. 19-22 mm, tip acute to rounded, up to c. 2 mm wide distally, wings exceeding capsule 0.5-1 mm distally, 3-4.5 mm proximally; dehiscence at margins of capsule body.

Distribution: North West Yunnan, c. 26-28° N, 99°40' E, in mixed temperate woodland in the Doyon-lumba region, between the Mekong and Salween rivers at an altitude of 2600 - 3400 m. See fig. 4.1.

Ecology & Biology: Found growing in shaded woody and rocky places by mountain streams in schist and sandy soils. Recorded in flower and fruit in August and September.

Discussion: When E. Irmscher first described *B. asperifolia* in 1927 he cited two specimens in the protologue, *Handel-Mazzetti* 9936 and 9599. Neither the type status,

nor herbarium were specified. In 1931 Irmscher, in *Symbolae Sinicae* VII: 389, edited by Handel-Mazzetti, again cited two specimens but this time they were *Handel-Mazzetti* 9939 and 9599, the latter of these being designated "typus". This is considered a lectotypification; the location of the specimen is WU, where Irmscher saw specimens and where Handel-Mazzetti worked. No specimens of *B. asperifolia* have been found with the number *Handel-Mazzetti* 9936, either in WU (Till, *pers. comm.*, 1997) or elsewhere and this citation in the original description should be considered a mistake (which has not been repeated). In 1939 Irmscher cited *Handel-Mazzetti* 9939 and 9599 among other specimens but he designated *Handel-Mazzetti* 9939 (E) as "*Typus der Art*". This should be ignored as his earlier lectotypification has priority.

The typical form of *B. asperifolia* is acaulescent but, as Irmscher recognised, there are several specimens which tend towards caulescense. These have been included within the variation described here but the possibility of hybridisation with *B. grandis* giving rise to such forms cannot be ruled out without field work and possibly molecular studies.

ADDITIONAL SPECIMENS EXAMINED: CHINA: TIBET: Rong Tö valley, above Inigu Zayul, 8000 ft, 22.xi.1933, *F. Kingdon-Ward* 11001 (B); **YUNNAN:** NW Yunnan, Chien-Chuan-Mekong Divide, 26° 40' N, 99° 40' E, 10-11000 ft, ix 1922, *G. Forrest* 22312 (E, K); Tsé-Kou, recd. Mar. 1912, *Abbé. Monbeig* s.n., (E, P [2]); Mekong-Salwin Divide, Londjrela, 3400 m, 28.ix.1938, *T. T. Yü* 23135 (E [2]).

4.5.3.1 *B. ASPERIFOLIA* IRMSCH. VAR. *TOMENTOSA* T.T.YU

PLACE OF PUBLICATION: Bull. Fan. Mem. Inst. Biol. n.s. 1 (2): 118 (1948).

TYPE: China, Yunnan, Kiukiang Valley (Taron), Lungzung, 1800 m, 19.viii.1938, *T. T. Yü* 19908 (holotype: KUN, isotype: E!).

DIAGNOSIS: Distinguished by leaves densely hispid above, red, tomentose below and Yü (1948) describes 5 male tepals and much smaller flowers.

DISTRIBUTION: NW Yunnan, in the Kiukiang valley at an altitude of 1800 m.

ECOLOGY: Yu (1948) states this variety was very rare at the type locality.

DISCUSSION: Without further material a decision cannot be made as to the status of this variety.

4.5.4 *B. FIMBRISTIPULA* HANCE

PLACE OF PUBLICATION: Journal of Botany 21:202 (1883).

TYPE: China, Cantonensis, Ting-u-shan, West River, 6.v.1882, *C. Ford* s.n. (herb. H. F. Hance Recd. 1887 no. 22114) (lectotype designated here: BM! - on same sheet as Rev. E. Faber s.n.); same details, *C. Ford* 6 (isolectotype: K!); Canton, in jugo, Lo-fau-shan, Sept. 1882, *Rev. E. Faber* s.n. (syntype: BM! - on same sheet as lectotype)

SYNONYMY: ***B. cyclophylla*** Hook.f., Bot. Mag. t. 6926, 1887; Forbes & Hemsley, *J. Linn. Soc.* 23: 321, 1886-8; Dunn & Tutcher, *Bull. Misc. Inform.* 10: 113, 1912; Chun & Chun (1939), *Sunyatsenia* 4: 23-24 [=*B fimbristipula* Hance]; Irmscher, *Mitt. Inst. Allg. Bot. Hamburg*, 10: 508, 1939.

TYPE: "t. 6926 of Bot. Mag., Hong Kong", sine coll. (holotype: K).

DESCRIPTION: **Acaulescent** - very shortly caulescent tuberous herb up to 35 cm tall. **Bulbils** not observed. **Stem** ± erect, 2-10(-33) mm; internodes up to 26 mm; **stipules** caducous, ovate-triangular, 1-2.5(-7) × 0.8-1.8(-2.8) mm, apex acuminate, margin fimbriate. **Petiole** 1.2-11.5 cm, hirsute to hispid, more so at apex; **leaf blade** hirsute, mainly on veins below, upper leaf surface pubescent, ± symmetrical, ovate to subrotund, 2.4-11.1× 2 -15 cm, leaf base ± equally cordate, lobes (2-)5 - 35(-55) mm deep, rarely overlapping, slightly spreading apart, apex acute - acuminate, margin irregularly bidentate with larger teeth at vein endings, venation palmate-pinnate of 4-6 main veins, c. 4 veins in each half. **Inflorescence** a terminal cyme, slightly asymmetrical dichasial, up to 7 flowered, usually bisexual, male flowers usually maturing first,; **bracts** caducous, ± glabrous, not differentiated, ovate to obovate, apex acute, margin dentate-fimbriate. **Male flowers: pedicels** 10-30 mm; **tepals** 4, pink, outer pair (sepals) oblong to broadly obovate, 7.5-12.5 × 6-10.5 mm, apex rounded (-acute), margin entire; inner pair (petals) oblanceolate to broadly obovate, 6.4-11 × 2.2-7 mm, apex rounded, margin entire; **stamens** 25-50, androecium subglobose, symmetrical, filaments fused basally

into a column, 0.6-1 mm, the free filaments arising from the top of the column, 0.6-1.2 mm, anthers obovoid, 0.4-0.8 × 0.4-0.8 mm, connective not extended, dehiscence through slits down entire length of pollen sacs. **Female flowers: pedicels** 8-20 mm, elongating in fruit; **tepals** 3 (one specimen with 5 tepals), pink, 2 subequal, ovate 6-8.4 mm, apex acute, margin entire; inner tepal oblanceolate, 4-5 × 2-4.6 mm, apex rounded, margin entire; **ovary** obovoid-cordate, 4-5 × 3 mm, 3 wings, triangular, 1 longer, upper margin ± horizontal, 3 locular, placentae axile, partially bilamellate (fide Irmscher, 1939), bearing numerous minute ovules on both sides; **styles** 3, persistent, united at base for 0.5-1.6 mm, whole style up to 3.2 mm, bifid, branches c. half length of style, a continuous papillose stigmatic band spiralling 1-2 times around each branch. **Capsule** becoming scarious, 7.2-11 × 8.5-23 mm, main body obovoid-cordate, 5.8-8.6 × 5.6-6 mm, wings 3, triangular, 1 longer, 4.5-18 mm long, upper margin ± horizontal, lower margin 14-24 mm, straight - convexly curved, tip acute to obtuse, 0.2-1.5(-2.0) mm wide distally, wings not exceeding capsule distally, c. 1 - 2.5 mm proximally; dehiscence at margins of capsule body.

CHROMOSOME NUMBER: 2n = 22 (Legro & Doorenbos, 1971).

DISTRIBUTION: S. & S.E. China: Zhejiang, Fujian, Jiangxi, Guangdong, Hong Kong; and Hainan (Chun & Chun, 1939), 60 - 1000 m. See fig. 4.1.

ECOLOGY & BIOLOGY: This herb grows on shaded water-dripping cliffs of bare rock by streams, in woods and on high rock, where the bulbs are hidden in cracks. The substrate has been noted as granitic and as calcareous.

There is one record of this species having scented flowers (*R. C. Ching* 2002).

VERNACULAR NAME: Tsze Pei Tien Kuei (Chun & Chun, 1939).

USES: Forbes & Hemsley (1886) recorded the following note, sent by Mr. Ford to Kew with his specimens: "Leaves of a *Begonia* used and sold by the priests at Tingushan monastery as a cure for fever, &c. The leaves are put in 'Samshin' (native spirit) and

allowed to remain some hours, when the liquor is drunk. The leaves are sold also in Peking, after being brought from Tingushan, where they have a great reputation."

Chun & Chun (1939) noted the following: "The diminutive form is invariably confined to rocky crevices on the higher slopes and, incidentally, is reputed to have a more potent curative property therefore preferred and more highly valued by herbalists. Because it commands a higher price in the drug market herb collectors often risk their lives to climb high cliffs and precipices to gather it. In recent times only the large-leaved form is seen for sale. The plant is employed as a decoction for the treatment of tuberculosis".

W. T. Tsang 21542 & 22895 noted that the medicine made from this species was called "Tin Kwai".

ADDITIONAL SPECIMENS EXAMINED: CHINA: ZHEJIANG (CHEKIANG): Nan Yen, south of Ping Yang, 60-175 m, June-July 1924, *R. C. Ching* 2002 (E [2], K, P, US); **FUJIAN:** Buong Kang, Yenping, 700 m, 8.vi.1925, *H. H. Cheung* 3258 (E); **JIANGXI:** Tong Shan, along Kwangtung border, near Sap-luk Po village, Waitsap District, 26.ix.1933, *W. T. Tsang* 22895 (P); **GUANGDONG:** Ting Wu Shan, 6.v.1928, *W. Y. Chun* 6398, (E); 60 miles west from the Port of Swatow, Thai-Yong, a mountain valley, surrounded by hills reaching 1000 ft and intersected by glens richly wooded: wet rocks and cliffs, 2000 ft, 17.ix.1899, *J. M. Dalziel* s.n. (E[2], K); Canton, Lo Fau Shan, 3200 ft, 15.viii.83, *Ford* s.n. (Com. 11/83 (Ex Hong Kong Botanical Gardens - K); In monte Dingwu-schan ad occid. urbis Kanton ad rupes, 700-800 m, 2.vii.19, 1.ii.17, 3.vi.16, R. Mell. s.n., *Handel-Mazzetti* 231 (WU); Septentr., in montibus Lungtou-schan, 60 km ad orientem urbis Siudsao ("Schautschou"), 800 m, 30.viii.1917, R. Mell s.n., *Handel-Mazzetti* 896 (WU); Hong Kong, Ma On Shan, 30.vi.1970, *S. Y. Hu* 10517 (K [2]); Ling Wu? Mt., 26.v.1918, *C. O. Levine* 2027 (E); Hown Hung Bui Ti'n gudi, Sam Kok Shan, Tsungfa-Lungmoon Districts, 18.v.1932, *W. T. Tsang* 20502 (US); Yam Na Shan (Yit Nga Shan), Mei (Kaying) District, 4-31.viii.1932, *W. T. Tsang* 21542 (P); Lin Fa Shan, Lin Fung Monastery, Hwei-yang District, 11-31.viii.1935, *W. T. Tsang* 25494 (E); Canton,

Lin Fa Shan, Lin Fung Monastery, Hwei-yang district, 11-31.viii.1935, *W. T. Tsang* 25553 (E).

4.5.5 A REASSESSMENT OF THE TAXONOMY OF *BEGONIA GRANDIS* DRYAND. (BEGONIACEAE) AND THE INFRASPECIFIC RANKS OF E. IRMSCHER

This section is in the format of a paper, with an introduction to *B. grandis*, a review of the cultivated and taxonomic history of the species, some comments on the problems of cultivated plant taxonomy and the infraspecific ranks used by Irmscher and a detailed taxonomic treatment of *B. grandis*. This paper will be submitted to *Edinburgh Journal of Botany*.

4.5.5.1 INTRODUCTION

In 1939, Irmscher published a monograph of *Begonia grandis* in which he gave a thorough review of the taxonomic history of this species and recognised several infraspecific taxa. Irmscher, however, did not feel that he could follow the usual rules regarding infraspecific taxa and instead outlined a new system which he hoped, although doubted, other systematists would follow. This system followed a military influenced terminology which was apparently fashionable at the time (Mill, pers. comm.). Partly as a result of these new infraspecific ranks and partly because Irmscher did not create an autonym, instead preferring a name which was in more common usage within horticultural circles at the time, several names were published which, today, cause some confusion.

B. grandis was first introduced into cultivation in Britain in 1804 (Sims, 1812; Brown, 1813) but it is clear that the species had already seen a long history of cultivation in China (Irmscher, 1939). This history, prior to its discovery as "new to science", causes further taxonomic problems for *B. grandis*.

In this paper I summarise Irmscher's findings on the cultivated history of *B. grandis* in China and Japan, discussing the implications for its typification, review Irmscher's use of infraspecific ranks and present a taxonomic treatment with lectotypifications,

distribution maps and full synonymy. I have chosen not to repeat a full review of the taxonomic history of the species and instead refer the reader to Irmscher's (1939) seminal paper.

4.5.5.2 A BRIEF HISTORY OF THE CULTIVATATION OF *B. GRANDIS* IN ASIA

Lange (1939), in his *History of the Begonia*, presents evidence that *B. grandis* has been recognised and esteemed in China for centuries as an ornamental plant in parks. Apparently, before the 14th century, this species was praised by Chinese writers and singers, as roses and lilies were by Western society. The popularity of *B. grandis* spread to Japan, when, according to Ito (1913), it was introduced from China in March in the eighteenth year of Kwan-ei (1641) into Nagasaki, Kyushu in southern Japan whence, at the beginning of Shoho (1644), it was propagated and introduced into Japanese gardens. Some evidence of the presence of *B. grandis* in Japan has also been found in Japanese art. Decaisne (1854) reported that *B. discolor* R.Br. (a synonym of *B. grandis*) was among the 23 most common cultivated plants which he recognised in paintings and a painted screen from the 17th century. Irmscher (1939) and Lange (1939) indicate that a Japanese art magazine, Kokka, included, in June 1891, an article on the Japanese painter, Maruyamo Okyo (1733 - 1795), with a full colour reproduction of a brush drawing of *B. grandis*, made by the artist in 1771.

4.5.5.3 TYPIFICATION PROBLEMS OF A CHINESE CULTIVATED PLANT

The first western recognition of *B. grandis* was made by Kaempfer in 1712, after his travels in Japan in 1691 & 1692 (Dandy 1958), when he presented the species under the Japanese name Sjukaido. Thunberg also collected the plant in Japan and published it under the name *B. obliqua* in 1784. Thunberg's specimen, present in Uppsala, represents the first collection of *B. grandis* and is therefore selected as the type of the species here. Dryander (1791) placed Thunberg's *B. obliqua* in synonymy of his *B. grandis* as Linnaeus had already laid claim to this name in 1753. Taxonomic confusion arose with

the publication, in 1811, of *B. evansiana* Andrews and then *B. discolor* R.Br. in 1813. Both these names were variously taken up by the scientific and horticultural communities, although the name *B. grandis* was still used by some people.

The description of *B. sinensis* by A. de Candolle in 1859 has, however, caused the greatest amount of perplexity. *B. sinensis* has been treated as a separate species to *B. evansiana*, e.g. Forbes & Hemsley (1886), as a synonym of *B. evansiana*, e.g. Clarke (1879) and as an infraspecific taxon within *B. grandis*, e.g. Irmscher (1939). This situation has arisen because the original material of *B. grandis* and *B. evansiana* was, most probably, from cultivated stock in Japan and China respectively and as Irmscher intimates, *B. sinensis* is likely to be the wild progenitor of the cultivated plants. A description based on material of a taxon that has been in cultivation for a considerable period of time (centuries in this case) is undesirable but not rare, e.g. *Malus spectabilis* (Aiton) Borkhausen, *Kerria japonica* (L.) DC., *Viburnum plicatum* Thunb. (C. Alexander, pers. comm.; D. Cann, pers. comm.).

It is possible, although not confirmed here, that there are very few truly wild plants that would fit the typical description of *B. grandis sensu stricto*. With this in mind, an important philosophical point is raised: should the autonym of a taxon be based entirely on cultivated material? If, as in this case, plants exist which appear to be the wild progenitor, then I would argue that they should be circumscribed within the same taxon. Irmscher (1939) implicitly dealt with this dilemma, but found a different solution.

Irmscher (1939) also failed to find any discrete boundaries to *B. grandis* and *B. sinensis*. These taxa were defined by a combination of characters which could individually fall outwith the given range and possessed completely overlapping distributions, therefore producing many intermediate forms. While Irmscher was studying *B. grandis*, he noted the existence of an until then undescribed taxon. This taxon had a distinct distribution and was consistently able to be distinguished from the rest of *B. grandis* except for a very few sheets from Western Yunnan and Sichuan and what was then Tibet. Irmscher

named this taxon *B. grandis* conta. reg. *holostyla.* With these different degrees of variation partitioning lies the crux of Irmscher's new system of infraspecific ranks.

4.5.5.4 THE INFRASPECIFIC RANKS OF IRMSCHER

In his paper on Chinese *Begonia,* Irmscher (1939,) discusses the various problems he has encountered with different terms used to describe infraspecific ranks; Du Rietz's (1930) terms variety and subspecies were, in practise, often difficult to differentiate; Turesson's (e.g. 1922) ecotypes referred to genetic units which reflect environmental conditions; the breeds of zoologists did not allow transitional forms at the boundaries of mutually exclusive areas. This discussion was in the context of *B. grandis* and *B. laciniata* Roxb. (now a synonym of *B. palmata* D.Don).

To solve this problem, Irmscher suggested a new system. First, a neutral expression is chosen as a "tribe descriptor" and then an adjective is used to express any special characters. Irmscher suggested the term "turma" ("ta." for short) which means 'squadron' to assign to a swarm or group. Geographically restricted subspecies (races) would then be defined by the size of their distribution, using the adjective "regionalis" ("reg.") or "localis" ("loc."), those with a suspected hybrid origin by "hybrida" (hyb."), those from a mutated origin with "mutata" ("mut.") and ecotypes denoted by "oecotypica" ("oetc."). Tribes with disjunct distributions could be indicated with the addition of the term "disjuncta" ("disj.") and those with a random distribution through their total area by the term "diffusa" ("diff."). Irmscher advises that further epithets could be formulated as required. To indicate the occurrence of transitional forms between the subspecies, the addition of a prefix, either "con" or "eu", would be applied to the word turma. The word "conturma" ("conta.") would indicate a form with transitions and the word "euturma" ("euta."), one without.

Despite the careful description of this new system of infraspecific ranks, Irmscher said he was convinced that it would be rejected by conservative systematists. Asking for flexibility to accommodate the needs of geneticists, Irmscher acknowledged that in

many cases simple ternary epithets (infraspecific epithets), likened to the zoologists' race classification, would suffice. In a final concession to the status quo, Irmscher accepted that the various "turma", in the case of further differentiation, could still be grouped into varieties, subvarieties, forms etc. (in the Englerian sense) and outwith the systematic presentation, could be represented in binary with an asterisk (*), as Ascherson and Graebner (1896-1939) had already suggested.

Prefix	"tribe descriptor"	Adjective
con	turma (ta.)	regionalis (reg.)
eu		localis (loc.)
		hybrida (hyb.)
		mutata (mut.)
		oecotypica (oetc.)
		disjuncta (disj.)
		diffusa (diff.)

TABLE 4.2 SUMMARY OF IRMSCHER'S INFRASPECIFIC TERMINOLOGY

4.5.5.6 TAXONOMIC TREATMENT: *B. GRANDIS* DRYAND. SUBSP. *GRANDIS* VAR. *GRANDIS*

PLACE OF PUBLICATION: Trans. Linn. Soc., 1: 163, 1791.

TYPE: "*Japonia Thunberg*" (lectotype designated here: UPS-Thunb, microfiche UPS-Thunb. 22354!)

Note 1: Dryander (1791) cites *Begonia obliqua* Thunb. *Japon.* 231. *defer. lc.* "*habitat in Japonia. Engelb. Kaempfer, Car. Petr. Thunberg.*"

Note 2: Juel (1918) confirms that Thunberg collected this specimen in Japan.

SYNONYMY:

Sjukaido Kaempf., *Amoen. Exot. Fasc.* 5: 888, 1712; Thunberg, *Fl. Jap.* 231, 1784 [= *obliqua sensu* Thunb. *non* L.]; Kaempfer, *Icon. Select. Pl.* pl. 20, May 1791; Dryander, *Trans. Linn. Soc.* 1: 164, 1791 [=*grandis* Dryand.]; A. de Candolle *Prodr.* 15(1): 313, 1864 [=*evansiana* Andrews]; T. Ito, *Icon. pl. japon.* 1(5), t. 20, 1913 [=*evansiana* Andrews]; Irmscher, *Mitt. Inst. Allg. Bot. Hamburg* 10: 492, 1939 [="*grandis* conta. *Evansiana* (Andrews) Irmsch."].

TYPE: Kaempfer's illustration in *Amoen. Exot. Fasc.* 5: 888, 1712 (lectotype designated here).

Note 3: Dandy (1958) states that Kaempfer's Japanese plants were collected in 1691 and 1692 and are in volume H.S. 211 of the Sloane herbarium (BM-SL). No Kaempfer specimens of *B. grandis* were located in either the Sloane herbarium or Oxford (OXF) (S. Marner, pers. comm.), the only known locations of specimens used for the drawings in the Amoenitates (Stafleu & Cowan, 1976 - 1988).

B. obliqua *sensu* Thunb., *Fl. Jap.* 231, 1784, *non* L., 1753; Kaempfer, Icon. Select Pl. pl. 20, May 1791; Dryander, *Trans. Linn. Soc.* 1: 164, 1791 [=*B. grandis* Dryand.];

A. de Candolle *Prodr.* 15(1): 313, 1864 [=*B. evansiana* Andrews]; C. B. Clarke in J. D. Hooker, *Fl. Brit. Ind.* 2: 638, 1879 [=*B. evansiana* Andrews]; A. R Franchet, *Pl. david.* cat. no. 387, p. 136, 1884 [=*B. evansiana* Andrews,]; T. Ito, *Icon. pl. japon.* 1(5), t. 20, 1913 [=*B. evansiana* Andrews]; Irmscher, *Mitt. Inst. Allg. Bot. Hamburg* 10: 492, 1939 [="*B. grandis* conta. *Evansiana* (Andrews) Irmsch."].

TYPE: "*Japonia Thunberg*" (lectotype designated here: microfiche: UPS-Thunb. 22354!)

B. evansiana Andrews, *Bot. Repos.* 10, pl. 627, June 1811; J. Sims, *Bot. Mag.* 36 t. 1473, 1812; A. de Candolle *Prodr.* 15(1): 313, 1864; A. R. Franchet, *Pl. david.* cat. no. 387, p. 136?, 1884; F. B. Forbes & W. B. Hemsley, *Index Florae Sinensis* I, in *J. Linn. Soc.* 23: 321, 1886; T. Ito, *Icon. pl. japon.* 1(5), t. 20, 1913; Irmscher in H. Handel-Mazzetti, *Symb. Sin.* 7: 388, 1931; Irmscher, *Mitt. Inst. Allg. Bot. Hamburg* 10: 492, 1939 [="*grandis* conta. *Evansiana* (Andrews) Irmsch."].

TYPE: *Bot. Repos.* 10, pl. 627, June 1811 (lectotype designated here).

Note 4: No herbarium specimens are known to exist for H. C. Andrews (Stafleu & Cowan, 1976 - 1988). Andrews (1811) states the drawing in *Bot. Repos.* 10 was made at Stepney in October 1810.

Note 5: Irmscher cites the year of publication as 1810 and not 1811.

Note 6: Andrews (1811) states that "we are also indebted to T. Evans, esq., whose collector discovered it growing about the sides and clefts of rocks near a waterfall in the interior of the Island of Pulo-Pinang in 1808." This statement of origin is most likely a mistake as C. B. Clarke indicates first in the *Flora of British India* (1879) and second in his treatment of Indian *Begonia* (1881), when he states that there is no example of this species from Pinang in the herbarium in Kew.

B. discolor R.Br. in Aiton, *Hort. Kew*, ed. 2, 5: 284, 1813 *nom. illeg.*; Steudel, *Nom. Bot.* 1: 104, 1821 [=*evansiana* Andrews]; A. de Candolle *Prodr.* 15(1): 313, 1864 [=*evansiana* Andrews]; F. B. Forbes & W. B. Hemsley, *Index Florae Sinensis* I, in *J. Linn. Soc.* 23: 321, 1886 [=*evansiana* Andrews]; Irmscher, *Mitt. Inst. Allg. Bot. Hamburg* 10: 492, 1939 [="*grandis* conta. *Evansiana* (Andrews) Irmsch."].

TYPE: Not located (TL-2 says most of the types are in BM and based on material from Kew)

Note 7: The citation of the authority of this species has been inconsistent. Steudel names Smith as the author of *B. discolor* but I have not managed to trace who Smith may have been. A. de Candolle cites 'W. Kerr *ex* hort. Kew'. William Kerr was a gardener at Kew (Stafleu & Cowan, 1976 - 1988), who probably collected in Guandong and Hong Kong in the year prior to his arrival in Kew (Desmond, 1994) and is cited as the collector, in 1804, of the original material for this name in Brown (1813). This confusion stems from the fact that R. Brown is known to have attached his name to the descriptions in Hort. Kew. While he did not write all the descriptions (Stafleu & Cowan, 1976 - 1988), the descriptions of *Begonia* are in class XXI and Stafleu & Cowan (1983) state that R. Brown did write new descriptions for classes XIII to the Cryptogams.

Note 8: Hooker (1899) confirmed that *B. grandis* was probably introduced to Kew in 1804 by the Honourable East India Company.

B. bulbifera hort. *ex* Steudel, Nom. Bot., 1: 104, 1821, *pro syn. B. evansiana* Andrews, 1811 (*nomen. inval.*, art. 34.1(c) ICBN); *non* Loddiges *ex* Otto & A.Dietr., 1841.

Note 9: Smith *et al.* (1986) cite Irmscher (1939) as synonymising this name; he does not.

Diploclinium evansianum (Andrews) Lindley, Veg. Kingd., ed. 1, 318, t. 220, 1846; A. de Candolle, Prodr. 15(1): 313, 1864 [=*evansiana* Andrews]; F. B. Forbes & W. B. Hemsley, Index Florae Sinensis I, in *J. Linn. Soc.* 23; 321, 1886 [=*evansiana* Andrews].

Note 10: Smith *et al.* (1986) cite Irmscher (1939) as synonymising this name; he does not.

Knesebeckia discolor (R.Br.) Klotzsch, *Monatsber. Königl. Preuss. Akad. Wiss. Berlin*, 122, 1854; *Abh. Kön. Akad. Wiss. Berlin*, 1854, p. 164, 1855; Klotzsch, *Begoniac.*, 44, 1855; A. de Candolle, *Prodr.* 15(1): 313, 1864 [=*evansiana* Andrews]; F. B. Forbes & W. B. Hemsley, *Index Florae Sinensis* I, in *J. Linn. Soc.* 23: 321, 1886 [=*evansiana* Andrews].

Note 11: Smith *et al.* (1986) cite Irmscher (1939) as synonymising this name; he does not.

B. sinensis A.DC., *Ann. Sci. Nat. Bot., sér.* IV, 11: 125, 1859; A. de Candolle, *Prodr.* 15(1): 313, 1864; C. B. Clarke in J.D. Hooker, *Fl. Brit. Ind.* 2: 638, 1879 [=*evansiana* Andrews]; F. B. Forbes & W. B. Hemsley, *Index Fl. Sinensis* in *J. Linn. Soc.* 23:323, 1886; L. Diels, *Bot. Jahrb. Syst.* 29(3+4): 479, 1900; Matsumura & Hayata, *Enum. Pl. Ins. Form.* in *J. Coll. Sci. Imperial Univ. Tokyo, Japan* 22:166, 1906; Léveille, *Cat. Pl. Yun-Nan*, p. 17, 1915; Irmscher in H. Handel-Mazzetti, *Symb. Sin.* 7: 388, 1931; T.T. Yu, Bull. Fan. Mem. Inst. Biol. n.s. 1(2): 120, 1948; Irmscher, *Mitt. Inst. Allg.* Bot. *Hamburg* 10: 494, 1939 [= "*grandis* conta. *sinensis* Irmsch."] **synon. nov.**

TYPE: China, in montibus prope Pekin versus templum Don - Schwari - ssy (herb. Fisch.! nunc Acad. petr.) holotype not located; same details,"ex herb. petrop. a Tatarinoff lect." (lectotype designated here: G-DC microfiche 15(1): 313.95!)

Note 12: Irmscher (1939) states that he could not find the specimen cited by A. de Candolle (1859; 1864) in LE.

"In Montibus prope Pekin versus templum Don - Schwari - ssy (herb. Fisch.! nunc Acad. petr.)"

The specimen is not present in G either (Burdet, pers. comm.) and so I have selected the specimen that is present in G-DC as a lectotype.

B. martini H.Lév., *Bull. Soc. Agric. Sarthe* 39: 323, 1904; Irmscher in Handel-Mazzetti, *Symb. Sin.* 7: 388, 1931, "*martinii*" [=*sinensis* A.DC.]; Irmscher, *Mitt. Inst. Allg. Bot. Hamburg* 10: 494, 1939 "*martinii*" [= "*grandis* conta. *sinensis* Irmsch."] **synon. nov.**

TYPE: China, Kouy-Tchéou, environs de Gan-pin, sous les grands rochers sur plombant une dépression en forme de cirque; fleurs roses, 20 sept. 1897, *L. Martin & E. Bodinier* s.n. (Holotype: B!)

Note 13: Internal evidence shows that Léveillé consistently 'latinized' Martin's name, hence '*martini*' is the correct orthography as in Art. 60C.2 of the ICBN.

B. bulbosa H.Lév., *Feddes Rep. Sp. Nov.* No. 131/133, 7: 21, 1909; Gagnepain, *Bull. Mus. Hist. Nat. (Paris)* 25: 282, 1919 [=*sinensis* A.DC.]; Irmscher in H. Handel-Mazzetti *Symb. Sin.* 7: 388, 1931 [=*sinensis* A.DC.]; Irmscher, *Mitt. Inst. Allg. Bot. Hamburg* 10: 494, 1939 [= "*grandis* conta. *sinensis* Irmsch."] **synon. nov.**

TYPE: China, Kouy-Tchéou, Yang-Kia-Tchong, sous bois, pentes, 25 juill. 1905, *J. Cavalérie* 2450 (holotype: E *n.v.*); China, Kouy-Tchéou, Majo et Kia tchong, 25.7.1907 *J. Cavalérie* 2450 (isotype: P); China, Kouy-Tchéou, Majo et Kia tchong, 5.7.1907, *J. Cavalérie* 2450 (isotype: P); China, Kouy-Tchéou, *J. Cavalérie* 2450 (isotype: P); China, Kouy-Tchéou, Yang-Kia-Tchong, bois pentes, 25.7.1905, *Cavalérie et Fortunat* 2450 (isotypes: P [2]).

Note 14: The holotype is currently on loan from E to PE.

B. erubescens H.Lév., *Feddes Rep. Sp. Nov. No.* 131/133, 7: 21, 1909; Gagnepain, *Bull. Mus. Hist. Nat.* (Paris) 25: 283, 1919 [=*evansiana* Hort.]; Irmscher in Handel-Mazzetti, *Symb. Sin.* 7: 388, 1931 [=*evansiana* Andrews]; Irmscher, *Mitt. Inst. Allg. Bot. Hamburg* 10: 492, 1939 [="*grandis* conta. *Evansiana* (Andrews) Irmsch."].

TYPE: China, Guizhou: "Kouy-Tchéou, environs de Gan-pin, dans le bois de He-che-teou, 8 août 1897, *L. Martin & E. Bodinier* 1793, (lectotype designated here: B! [female flowers]; isolectotypes: P! [3]); "Kouy-Tchéou, environs de Gan-Pin, pic de He-Che-Teou, sous bois au sommet, pied des rochers, 20 sept. 1897, *L. Martin & E. Bodinier* 1854 (syntype: B! [fruit] P! [2] [fruit]); la rivière Leao-Mié, 20 août 1897, *J. Cavalérie* 3283 (syntype: E! [fruit]); la rivière Leao-Mié, 20 août 1907, *J. Cavalérie* 3283 (syntype: P! [fruit]).

B. sinensis* var. *haematoneura Franch. ex Gagnepain, *Bull. Mus. Hist. Nat. (Paris)* 25: 283, 1919 *pro. syn.* [=*evansiana* hort.] (*nomen. inval.*, Art. 34.1c ICBN); Smith *et al. Smithsonian Contr.* 60: 233, 1986 *orthog error.* "*sinensis* var. *haemaloneura*" [=*erubescens* Lévl.] **synon. nov.**

Note 15: Gagnepain cited this name as a synonym of *B. evansiana* hort. but having checked *Pl. david.* (Franchet, 1884) and *Pl. delavay.* (Franchet, 1889-90) and *Enum. Jap.* (Franchet & Savatier, 1875), I have not found any mention of this variety. Specimens with the said name have been found in several herbaria and those in Paris were enclosed in type covers. The name is invalid as cited as a synonym.

B. grandis conta. ***evansiana*** (Andrews) Irmsch., *Mitt. Inst. Allg. Bot. Hamburg* 10: 492, 1939.

B. grandis conta. ***evansiana*** var. ***simsii*** Irmsch. *Mitt. Inst. Allg. Bot. Hamburg* 10: 493, 1939 **synon. nov.**

TYPE: J. Sims, *Bot. Mag.* 36, pl. 1473, 1812 [=*evansiana* Andrews] (lectotype designated here: pl. 1473, Bot. Mag. 1812!); Bonpland, Descr. des plant. rar. cult. à Malmaison et à Navarre. Paris 1813, p. 154, pl. 63 (syntype).

Note 16: Irmscher cited the two illustrations, designated here as types, as synonyms of his new variety. I have treated them as syntypes and designated the *Bot. Mag.* illustration as a lectotype due to its greater availability in libraries.

Note 17: Irmscher's treatment of these illustrations at the varietal taxonomic level is seen as inappropriate here. The choice of a cultivar status may have been more appropriate.

Note 18: In the protologue for this variety, Irmscher (1939) says that it was cultivated in European gardens at the beginning of the previous century. He has only met such staminal column lengths among cultivated material and he indicates that he takes the characteristic large flower as a product of cultivation. I do not accept Irmscher's derivation of a 5 cm diameter flower from the illustrations he cites as I found no evidence of flowers of this size in the herbarium material of horticultural plants that I examined during the course of this study (unless 1 cm of shrinkage can be accepted). The staminal column length that Irmscher gives as a diagnostic character of this variety is encompassed in the variation described here.

B. grandis Dryand. conta. ***sinensis*** (A.DC.) Irmsch., **synon. nov.** Mitt. Inst. Allg. Bot. Hamburg, 10: 494, pl. 13, 1939.

B. grandis subsp. ***evansiana*** (Andrews) F.A.Barkley & Golding, Sp. Begoniaceae, ed. 2, p. 48, 1974, **synon. nov.**

B. grandis subsp. ***evansiana*** var. ***simsii*** (Irmsch.) Golding & Kareg. in L.B.Sm., Smithsonian Contr. Bot. 60: 174, 1986, **synon. nov.**

B. grandis subsp. ***evansiana*** (Andrews) F.A.Barkley & Golding, Sp. Begoniaceae, ed. 2, p. 48, 1974, **synon. nov**.

B. grandis subsp. ***evansiana*** var. ***simsii*** (Irmsch.) Golding & Kareg. in L.B.Sm., Smithsonian Contr. Bot. 60: 174, 1986, **synon. nov**.

B. grandis var. ***simsii*** (Irmsch.) F.A.Barkley & Golding, Sp. Begoniaceae, ed. 2, p. 48, 1974, **synon. nov.**

B. grandis subsp. ***sinensis*** (A.DC.) F.A.Barkley & Golding, Sp. Begoniaceae, ed. 2, p. 48, 1974, **synon. nov.**

MISAPPLIED NAMES: ***Platycentrum discolor*** (R.Br.) Miquel, *Fl. Ned. Ind.* 1.1: 694, 1856.

Note 19: Smith *et al.* (1986) cite Irmscher (1939) as synonymising this name; he does not.

Note 20: There has been some confusion over the distribution of *B. grandis*, with several authors including Java within the geographic range of the species. Miquel appears to be the source of this error as he gives a Blume specimen from Java as a representative specimen of his *Platycentrum discolor*. A. de Candolle perpetuated this error when he cited *B. discolor* Blume as a synonym of *B. evansiana*. *B. discolor* Blume is a synonym of '*B. robusta* ?', which does occur in Java.

DESCRIPTION: Caulescent, tuberous herb up to c. 75 cm tall. **Bulbils** often produced. **Stem** erect, up to 18 mm diam.; internodes up to 22 cm; **stipules** deciduous (-tardily so), oblong-obovate to ovate-triangular, (2.6-)4-10(-13) × (1.2-)1.5-3.4(-5) mm, apex acute (- rounded), margin entire. **Petiole** tinged red, 1-23 cm, ± glabrous. **Leaf blade** green, red or with reddish veins below, ± glabrous - sparsely hispid - pilose, - densely pilose on lower veins, strongly asymmetric, ovate - broadly ovate, 3.3-20 × 2.5-18 cm, leaf base with deeply cordate, unequal lobes, (0.5-)1.0-3.5(-4.5) cm deep, occasionally

overlapping at petiole apex, diverging, apex gradually acuminate (- acute), margin shallowly angularly repand, bidenticulate - dentate - biserrulate - serrulate, largest teeth at vein endings, palmate-pinnate venation, 3-6 main veins, 3-4 veins reaching the margin in small lobe, 6-7 in large lobe. **Inflorescences** axillary and terminal, racemose, (3-)4-10(-14) cm, unisexual or bisexual, male flowers usually maturing first, 3-20 flowers, partial inflorescences asymmetric dichasia, 3-9 flowers; **bracts** deciduous, glabrous, stipule-like on main stem, at partial inflorescence first branching points broadly ovate-obovate (4-)6-10(-12) × 3-7.2(-12) mm (tend to be bigger in cultivated material), apex rounded - truncate, margin entire, at later branching points, oblong - obovate, 2.8-4 × 1.6-3 mm, apex rounded, margin entire. **Male flowers: pedicels** 14-36 mm **tepals** 4, pink, outer pair (sepals) oblong-ovate to broadly ovate, 8-14.5(-20) × 6.5-14 mm, apex acute - rounded, margin entire; inner pair (petals) (ob)lanceolate - (ob)ovate, 5.5-10 × (2.2-)4-8 mm, apex acute - rounded, margin entire; **androecium** globose, symmetrical; stamens 20-70, filaments fused basally into a column, (1-)1.4-4(-6.6) mm, the free filaments arising from the upper part of the column, 0.6-1.4 mm, anthers obovoid-ellipsoid, 0.6-1.0 × 0.4-0.8 mm, connective not extended, dehiscing through slits down entire length of pollen sac. **Female flowers: pedicels** 16-28 mm, elongating in fruit up to 40 mm; **tepals** 3 or 5, pink, 2 or 4 tepals subequal, broadly (ob)ovate, 5.6-11(-16) × (4-)5.8-9.8(-14) mm, 1 tepal smaller, innermost, 4-7.4(-10) × 1.6-2.5(-6.8) mm (ob)lanceolate, apices rounded - acute, margins entire, spreading; **ovary** ellipsoid, 7.2-12 × 3.6-5.5 mm, 3 wings, triangular, 1 longer, extending upwards, 3-locular, placentae axile, mostly bilamellate, bearing numerous minute ovules on both sides; **styles** 3, persistent, briefly united at base for 0.6-1 mm, whole style 2.4-3.6 mm, bifid, the branches erect, slightly spreading, 0.25-0.5 mm length of whole style, a continuous papillose stigmatic band curved around outer base of branches then encircling each branch, tending to spiral once around top of branches. **Capsule** 19-23 × 15-31 mm, becoming scarious, main body ellipsoid - narrowly so, 11-15 × 4.5-8 mm, wings 3, triangular with elongated tips, one longer, upper margin 12-23 mm, lower margin ± straight - sigmoid, 22-38 mm, upper margins straight (- repand), ± horizontal -

mm, wings 3, triangular with elongated tips, one longer, upper margin 12-23 mm, lower margin ± straight - sigmoid, 22-38 mm, upper margins straight (- repand), ± horizontal - ascending up to 45°, tip obtuse - acute, 1-2.4 mm wide distally, wings exceeding the capsule 0.6-1 mm distally, 2-5 mm proximally, dehiscence at margins of capsule body. **Seeds** oblong-ellipsoid c. 0.4 mm.

CHROMOSOME NUMBER: 2n = 26 (Matsuura & Okuno, 1936; *et al.*, 1946; Legro & Doorenbos, 1971); 2n = 24 (Bowden, 1945).

DISTRIBUTION: China: Fujian, Guizhou, Hebei, Hubei, Jiansu, Jiangxi, Qinghai, Shandong, Sichuan, Yunnan, Zhejiang. See fig. 4.2.

FIG. 4.2 MAP TO SHOW DISTRIBUTION OF *B. GRANDIS* SUBSP. *GRANDIS* AND *B. GRANDIS* SUBSP. *HOLOSTYLA*.

ECOLOGY & BIOLOGY: This subspecies is widely cultivated, being grown in and around temple complexes. It is often found growing along roadsides, either by cultivation or as a 'weed'. In more natural habitats it grows in humid, shaded, rocky

(including quartzite) areas, even in wet caves, in forested areas and on dry slopes and ravines with *Thuja* and *Quercus*.

VERNACULAR NAMES: **Beni-ito-bana** *pro. syn. evansiana* in T. Ito, *Icon. pl. japon.* 1(5), t. 20, 1913. **Ning sha tung / Tsching shan Kay** *teste A. Engler* 7048 (B). **Shûkaidô / Sjukaido:** Kaempfer, Amoen. Exot. Fasc., 5: 888, 1712, writes that, in Japan, this is both the common and literate name for this plant (*vulgo & literatis*); Japanese name in T. Ito, *Icon. pl. japon.* 1(5), t. 20, 1913. **Tsieou-hai-tang / Tsou Hoy Tong** (=Autumnal Hai-tang): Dryander, Trans. Linn. Soc., 1: 163, 1791 explains how this is a volume of drawings in Sir. Joseph Bank's library. The drawings were done in Canton by a Chinese person who had been taught botanical illustration by a Mr. Blake. J. Sims, Bot. Mag., 36, pl. 1473, 1812 gives this as the Chinese name in cultivation; *Mem. Hist. Chin.*, 3: 443; R. Brown in Aiton's *Hort. Kew*, 2nd Edn, 5: 284, 1813; A. de Candolle, *Prodr.* 15(1): 313, 1864. **Yôraku-sô** Nom. hort. in Yedo (ie. Tokyo) in T. Ito, *Icon. pl. japon.* 1(5), t. 20, 1913.

USES: Horticultural

ADDITIONAL SPECIMENS EXAMINED: CHINA: BEIJING & HEBEI (HUPEI): Jietansi temple, ca. 35 km W of Beijing, above the temple complex, ca. 300 m, 29.viii.1984, *Bartholomew & Boufford* 2067 (E); Mountains west of Peking, summer 1881, *W. Bretschneider* 95 (BM); "Spratenca in euvatopsis prope Pexin in China boreal, Keridoir, *herb. Al. de Bunge* (P); Peking, Western Hills, Aug. 1882, *W. R. Carles* 93 (E); Peking, Western Hills, 16.viii.1885, *W. R. Carles* 107 (E); Peking, 1882, *W.R. Carles* s.n. (BM); Tche-Ly, 38° N, rochers ombragés, humides ire Kia Chan et du Ping Chan, Aug. 1910, *L. Chanet* 557 (E); Tche-Ly, Ping Chau, rochers ombragés, Aug. 1910, *L. Chanet* s.n. (?); Tche-Ly-Fou Ping, Aug. 1910, *L. Chanet* s.n. (?); 500 km env. au Sud de Pekin, 1903-1935, *Chanet & Serre*, Peres Lazaristes s.n. (P [2]); Wofussu, Western Hills, 26.9.1920, *N. H. Cowdrey* 1024 (K); environs de Pekin (Chine septentrionale), 1865, M. l'Abbé *A. David* 410 (P [3]); Chili Prov., Western Hills, Aug 1930, *Dorsett & Morse*

7001 (B); Chili Province, Western Hills, Aug-Oct 1930, *Dorsett & Morse* 7185 (B); Peking, *Hemeling* 49 (E); Moyen & Bas Hoang Ho & Pai Ho, Kiaoshan, Shanhaikwan, 28.viii.1915, *R. P. Licent* 1527 (P); Peking, Western Hills, *W. Pudom* s.n. (K); Pavin est de la pagoda peuter, nord du Kia Chan, Aug 1930, *Kiu Yang* 3214 (P); **SHANDONG (SHANTUNG):** Cultivated in temple yard, 30 m, 13.viii.1930, *C. Y. Chiao* 2907 (E); Lung Tung, Tsinanfu, 300 m, 8.ix.30, *C. Y. Chiao* 3088 (K, E); Meng Shan, Fei Hsien, 350 m, 17.viii.1936, *Cheo & Yen* 399 (P); Kiantshou, Tsingtan, Lauschangebirge: wald beim Tempel Ming-hsai-tung, 500 m, 26.vi.1913, *A. Engler* 7048 (B); Tsingtan, Kiautschou, 5-10 m, 27+28.vi.1913, *A. Engler* 7103 (B); T'ai Shan Mountains, Ta ianfu, 4-9.ix.1912, *M. Strong Clemens* 1446 (E); **JIANGSU (KIANGSU):** 28.x.20, *Bau Hwa Shan* 576 (E); **ZHEJIANG (CHEKIANG):** N. Yentang, Wenchow, 400 m, 15.viii.1920, *H. H. Hu* 22 (B); Tien-mu-shan, 25.ix.1947, *Y. W. Law* 827 (K); **FUJIAN (FUKIEN):** "Collected on *Mr. Dunn's* expedition to Central Fokien, April to June 1905", *Hong Kong no.* 2716 (B [2]); Kushan near Foochow, 500 m, 7.viii.1925, *H. H. Chung* 3715 (E); **JIANGXI (KIANGSI):** prope oppidum Ningdu loco lapidoso infra templum, Mt.s Lienhwa-shan, c. 800 m, Jul/Aug 1921, *Wang-Te-Hui, herb. Handel-Mazzetti* 459 (E, WU [2]); Lu Shan, Huang Yen Ssu, 13.viii.1932, *H. C. Cheo* 74 (E); **GUIZHOU (KWEICHOW / KOUY-TCHÉOU):** Kouy-Tchéou, *E. Bodinier* s.n. (P); China, Ping-fa, 25.iii.1902, *J. Cavalérie* 883 (E); environs de Gan-pin, sous la Grande Grotte, 26.viii.1898, *Martin & Bodinier* s.n. (P [2]); Tsunyi Hsien, Liang Feng Yah, 900 m, 3.viii.1931, *Steward, Chiao & Cheo* 146 (L); Ta Ho Yen, Fan Ching Shan, 900 m, 17.ix.1931, *Steward, Chiao & Cheo* 638 (K, L); **HUBEI (HUPEH):** Patung Hsien, 30.vii.34, *Ho-Ch'ang Chow* 1056 (E); Ichang, Nan-t'o and mountains to northward, *A. Henry* 2110 (P); Ichang, *A. Henry* 6236A (P); Patung, Aug. 1901, *E. H. Wilson* 2259 (B, E, K, P); Aug. 1901, *E. H. Wilson* 2438 (B, K); Hsiang Shan, Fang, Aug. 1901, *E. H. Wilson* 2458 (B, K); **SHAANXI:** Taihangshan, Toukoutwei, 19.vi.1915, *R. P. Licent* s.n. (P); **QINGHAI:** "Ile D'or-Chin, belles fleurs roses Londre Je l'ui déja rue dans le jardin d'un Mandarin à Ching hae, près Ming Po", 1844, *M. Leclaucher* s.n. (P); **SICHUAN (SZECHWAN):** Pao-hsing-hsien, 2400 m, 2(?5).viii.1936, *K. L. Chu* 3624 (E); Lu-shan-hsien, 1100 m, 18.x.1936, *K. L. Chu* 4030

(P); Mount Omei, 4500 ft, recd. Dec. 1887, *Rev. E. Faber* 492 (K); Omei Hsien, Mt. Omei, 1500-2000 ft, 2.viii.1928, *W. P. Fang* 2381 (K, P); District de Tchen-Keou-Tin, lieux humides nom chinois Ja' houng pas ? comme peitoral, 1400 m, *R. P. Farges* 56 (P [3]); District de Tchen-Keou-tin, ta hong pao, 1400 m, juillet, *R. P. Farges* 668 (BM, P [2]); **YUNNAN:** *E. E. Maire* 5 (E); Yun-nan-sen, recd. Nov. 1906, *E. E. Maire* 985 (E); Yun-nan-sen, recd. Nov. 1906, *E. E. Maire* 2391 (E); **CHINA UNKNOWN:** hai Tam Buo, *D'Argy herb Leveille* s.n. (E); China, 1880-1881, *Bretschneider* 216 (P); s.l., ex herb. *Ad. Brongniart* (P); Kewkiang Hills, 6.ix.1891, *W. R. Carles* 107 (E); Kuikiang Hills, Russian Bungalow, 23.viii.1891, *W. R. Carles* 107 (?30) (E); Hab. in China, *Martin* s.n. (L); Kiukiang an Yangtse, *O. von Mollendorff* 42 (B [2]); Mai 1821, herb. *Poiret* (P); China, Yen tze Vreou, Juillet 1891, *A. Provost* 33 (P); China, Pouo-hoa-chan, versauts ombres, Juin 1891, *A. Provost* 109 (P [2]); Insul. matinca, cult., 22.iv.1890 s.l. s.n. (L); **JAPAN:** Japan, Tokio cultivé, Juin 1928, *Alleizette* s.n. (L); Yokohama, "I think cultivated", recd. May 1876, *F.V. Dickins* 2050 (K); ex herb. Yedo, herb. *E. Drake* 1046 (P [3]); Japan, jardin des Frères de Marie à Tokyo, 5.8.1890, *M. l'Abbé Faurie* s.n. (P); Yokohama, Hakone, ex herb. Hort. Bot. Petropolitani, 1862; LINN 1125.2; *Maximowicz* s.n. (BM); Japonia *Siebold* s.n. (L); Tokio-cult., Août 1887 (P); Sakawa, Province Tosa, Science College, Imperial University, Sept. 1891 (K); '*Begonia obliqua* Thu' (L); s.l. s.n. (L); Tokyo, June 9, Acc. 23.iii.1960 (B); **HORT.:** Hort. *Th. H. A. J. Abeleven* (L); Cult., Rossdorf, Kwekeriy Kayser & Seibert, 15.viii.1957, *B. K. Boom* 34612 (L); ex herb. horti Petropolitani, *Bretschneider 313?* (B); Sand?i de St. Cloud, Sept. 1821, ex herb. *Ad. Brongniart* (P); Le Mans, hôtel Place Girard à Sté Croise, 10.x.1859, *H.Léveillé* s.n. (E); '*Begonia discolor*', Hort. Kew, 1829, herb. *E. E. Maire* (P); '*B. discolor*', Hort. Kew. *Evansiana*, B. Mag., 1830, herb. *E. E. Maire* (P); 1856, herb. *G. v. Martens* s.n. (B); Stuttgart, 15.viii.1830, herb. *G. v. Martens* s.n. (B); Bot. Gart. Berlin-Dahlem, 4.vi.1963, *Ra* 101 (B); '1820 Ex horto proprio Vogessachu', *A. W. Roth* von Naturhistorischen Museum zu Oldenburg durch Kauf erworben 1825 (B); Hort. Bot. Dahlem: 9, 31.viii.22, *R. Schlecter* s.n. (B); '*Begonia discolor*', Hort. *Schoenbaum Schott* mis? (B); Bot. Gart. Berlin-Dahlem, 15.ix.1982, *Schwerdtfeger* 12732 (B [2]);

Hort. Dahlem, 23.ix.11, *H. Strauss* s.n. (B); Hort. Berol., Jul. 1853, (B); Hort. Bot. Berol., 19.ix.1854, (B); Hort. Bot. Berol. (B); Hort. Carbr. (B); Hort. Paris., Sept. 1847 (B); Hortus Leidensis (L); Zweissteflauza in Garten, *B. discolor*, Oct. 1843 (B); '*B. discolor* Rob. Brown', HG 29/7-23 (B); '*Begonia discolor* R.Br.' (E); '*Begonia discolor*' (L); '*discolor*'(B).

4.5.5.7: *B. GRANDIS* DRYAND. VAR. *UNIALATA* IRMSCH.

PLACE OF PUBLICATION: Mitt. Inst. Allg. Bot. Hamburg 10: 493, 1939 "*grandis* conta. *Evansiana* var. *unialata*".

TYPE: China, Western China, 4000 ft, Sept. 1903, *E. H. Wilson* 3657 (lectotype designated here: HBG! isolectotypes: K! P!).

SYNONYMY:

B. grandis conta. ***evansiana*** var. ***unialata*** Irmsch., Mitt. Inst. Allg. Bot. Hamburg 10: 493, 1939.

B. grandis subsp. ***evansiana*** var. ***unialata*** (Irmsch.) Golding & Kareg. in L.B.Sm. *et al.*, Smithsonian Contr. Bot. 60: 174, 1986.

DIAGNOSIS: (translation of Irmscher's (1939) diagnosis)

Capsule with one large wing oblong to triangular-oblong, 15-17 mm long, middle 6-7 mm wide, apex often slightly acute, other wings strongly reduced, narrow ribs produced or ± absent.

DISTRIBUTION: Western Sichuan, c. 4000 ft.

ECOLOGY & BIOLOGY: The specimen was found growing on a rock.

4.5.5.8 *B. GRANDIS* DRYAND. VAR. *PUBERULA* IRMSCH.

PLACE OF PUBLICATION: Mitt. Inst. Allg. Bot. Hamburg 10: 496, 1939, "*grandis* conta. *sinensis* var. *puberula*."

TYPE: China: Hubei: 1885-88, *A. Henry* 2707 (lectotype designated here: B! isolectotype: E *n.v.* K! P!); *E. H. Wilson* 1598 (syntype: K *n.v.*)

SYNONYMY:

B. grandis subsp. ***sinensis*** var. ***puberula*** Irmsch.; F.A.Barkley & Golding, 1974.

DESCRIPTION (translation of Irmscher's (1939) diagnosis): Stem erect, slender, fine, strongly bent and flexuous above, provided with many buds, 30-40 cm long. Leaves doubly pilose above, covered with scattered, short, bristles, 0.4-0.6 mm long, moderately thick, and minute white hairs, densely puberulous, pale green below, outline oblong-ovate - oval, 5-10 cm long 2.5-5 cm wide, doubly serrate, often longly acuminate, base strongly oblique. Inflorescence few flowered. Staminal column 1.5-1.8 mm long; anthers 0.5-0.6 mm long.

DISTRIBUTION: West Hubei.

4.5.5.9 *B. GRANDIS* DRYAND. SUBSP. *HOLOSTYLA* IRMSCH.

PLACE OF PUBLICATION: Mitt. Inst. Allg. Bot. Hamburg 10: 498, pl.s 14, 15, 1939, "*grandis* conta. reg. *holostyla*"; Golding & Karcg. in L.B. Smith *et al.*, Smithsonian Contr. Bot. 60: 174, 1986.

TYPE: China, Sichuan, Muli Kingdom, Mount Mitzuga, 2970 m, Sept. 1929, *J. F. Rock* 18322 (lectotype designated here: US! isolectotype: B!); Muli Kingdom, 10-14000 ft, June 1922, *J. F. Rock* 5532 (syntype: E isosyntype: P!); Muli Kingdom, mountains between the Litang and Shou-Chu rivers, between Wa-Erh-Dje and Garu, 3080 m, July-August 1928, *J. F. Rock* 16906 (isosyntypes: B! E! syntype: US); prope monasterium

Muli as septentr. pagi yünnanensis Yungning, in regionis clalide temperatae fruticetis densis, alt. 2800 m, 31.vii.1915, *Handel-Mazzetti* 7353 (syntype: WU!); **Yunnan**, Les Gorges de San tchang Kiou, 11.ix.1889, *M. l'Abbé Delavay* 3924 (syntype: herb. Manila, ex herb. Paris isosyntypes: P [2]!); Yunnanfu, *Rev. P. Ducloux* 240 (syntype: K!); environs de Yun-nan-sen, bord des routes sous buissons, 12.vii.1904, *Fr. Ducloux* 2801 (syntype: herb. Manila, ex Paris isosyntypes: P [2]!); eastern flank of the Tali range, 25° 40' N, 8-10000 ft, July 1906, *G. Forrest* 4675 (syntype: E! isosyntype: P!); eastern flank of the Lichiang Range, 27° 30' N, 10-11000 ft, Aug 1910, *G. Forrest* 6383 (syntypes: E [2]! isosyntype: P!); eastern flank of the Lichiang Range, 27° 30' N, on the eastern flank of the Lichiang Range, 10-11000 ft, Aug. 1910, *G. Forrest* 6421 (isosyntype: BM! syntype: E!); south end of the Tengyueh valley, 25° N, 6000 ft, July 1912, *G. Forrest* 8738 (syntype: E!); Yang-pe mountains, 26° 45' N, 9000 ft, Sept. 1913, *G. Forrest* 11106 (syntype: E!); 1930-31, *G. Forrest* 28485 (syntypes: E [2]!); 1930-31, *G. Forrest* 28898 (isosyntype: BM! syntypes: E [2]!); in regionis calide temperatae ad austro-orient. pagi Dschungdien (Chungtien) rupibus infra vicum Hungschischao, alt. 2500-2700 m, 16.viii.1914, *Handel-Mazzetti* 4810 (syntype: WU!); ad viam Yünnanfu-Dali (Talifu), in regionis calide temperatae dunetis umbrosis inter vic. Mongschipu et Beyin-se prope Gwangtung, alt. 1900-2150, 6.ix.1914, *Handel-Mazzetti* 4890 (syntype: WU!); in regionis calide temperatae ad orientem fluminis Dsolin-ho cespitosis prope opp. Houd-jing, alt. 2150 m, *Handel-Mazzetti* 4941 (syntype: WU!); inter vicos Yanggai et Ilwadung, alt. 2050, 8.ix.1914, *Handel-Mazzetti* 4960 (syntype: WU!); Yun-nan-sen, au pied des roches humided hauts pies, Aug, *E. E. Maire* 738 (syntype: E!); Yun-nan-sen, rochers humides, Aug, *E. E. Maire* 894 (isosyntype: BM! syntype: E!); Yun-nan-sen, 1902 *E. E. Maire* (syntype: E); Yun-nan-sen, Sept., *E. E. Maire* 2340 (syntype: E!); Yun-nan-sen, Aug., *E. E. Maire* 2550 (syntype: E!); Yun-nan-sen, July, *E. E. Maire* 2551 (syntype: E!); pied des rochers, montagnes derrière Tong Tchouan, 2700 m, Sept. 1919, *E. E. Maire* 2715 sérié B (syntype: B!); mêmes localites que 3280, July 1910, *E. E. Maire* 3281 sérié B (syntype: B! isosyntype: Manila); mousse des rochers derrière Song Tchouen, 2700 m, Aug. 1910, *E. E. Maire*

3422 série B (syntype: B! isosyntypc: Manila); rochers des mont. derrière Song-Tchouan, 2600 m, Sept. 1913, *E. E. Maire* s.n. / 591 (syntype: E! isosyntype: WU); sur la mousse de rochers mont. derrière Song-Tchouan, 2700 m, Oct., *E. E. Maire* s.n. (syntypc: B!); pied des rochers à mi-mont de Kiao-mé-ti, 3100 m, Juillet, 1914, *E. E. Maire* s.n. / 117 (syntypes: E [2]! isosyntype: P!); rochers des mont. à Ma-hong, 2800 m, Sept., 1913, *E. E. Maire* s.n. / 570 / 868 (isosyntype: BM [2]! syntype: E[3]!); mont. neigeuse du Io-chan, 3400 m, Sept. *E. E. Maire* s.n. (syntype: E); rochers de Pan-long-sé, 2450 m, Nov., *E. E. Maire* s.n. (syntype: E! isosyntype: P!); Region of Tungshan, Yangtze drainage basin, east of Likiang, 1923, *J. F. Rock* 10526 (syntype: E!); Near Ngazi, drainage basin of the Yangtze, west of Likiang, Aug. 1923, *J. F. Rock* 10581 (syntype: E! isosyntype: California); mountains of Ludu, northwest of Li-Kiang, west of the Yangtzc, 2775 m, Aug 1929, *J. F. Rock* 18503 (isosyntypcs: B! P! syntypc: US); in rupestr. umbrosis collium occident prope Lichiang fu, 3000 m, 11.viii.1914, C. Schneider 2241 (syntype: B! isosyntypes: K! WU!); in locis umbrosis subhumidis ad hab. mont. Tsang prope Tali, 3000 m, Aug. 1914, *C. Schneider* 3099 (syntype: B! isosyntypcs: K! WU!); in locis humidis umbrosis in vallc flum Yangtze inter Chung tsien et Lichiang, 1800 m, Aug 1914, *C. Schneider* 3248 (syntype: B! isosyntype: K!); in rupibus calc. montis Hsi in locis umbrosis, 2200 m, 7.viii.1916, *O. Schoch* 282 (syntype: B! isosyntypes: K! WU!); Yangze, 1920, *S. Tén* 108 (syntype: E!).

SYNONYMY:

B. sinensis *sensu* Hook.f. in Bot. Mag. Ser. 3 55, t. 7673, 1899, non A.DC., 1859.

B. yunnanensis *sensu* Gagnep., Fl. Indo-Chine 2(8): 1098, 1921.

B. holostyla *sensu* F.A.Barkley & Golding, Sp. Begoniaceae, ed. 2, p. 48, 1974.

DESCRIPTION: Caulescent tuberous herb up to 60 cm tall. **Bulbils** often produced. **Stem** erect, up to 6 mm diam.; internodes up to 17 cm; **stipules** tardily deciduous, oblong-ovate triangular - oblong-triangular, 4-12.2 × 1.6-4.4 mm, apex acute - rounded,

margin entire, rarely denticulate-ciliate - serrulate. **Petiole** (0.4-)0.9-16 × 0.1-0.4 cm, glabrous - sparsely pilose; **leaf blade** upper surface ± glabrous - sparsely scabrid, lower surface sparsely hirsute - ± glabrous on veins, strongly asymmetrical, (broadly ovate -) ovate-triangular (1.5-)3.2-11 × (0.9-)2.2-10.4 cm, leaf base ± equally cordate, lobes (0.2-)0.5-2.5 cm deep, rarely touching, diverging, apex (acute -) gradually acuminate, margin occasionally angularly-repand, (bi-)serrate - (bi-)dentate - (bi-)denticulate, largest teeth at vein endings, palmate-pinnate veination, 4-5 main veins, 4-5 veins reaching margin in small lobe, 6-7 in large lobe. **Inflorescences** axillary and terminal, racemose, (1.8-)3.5-10(-14) cm, usually bisexual, male flowers usually maturing first, 6 - 20 flowers, partial inflorescences asymmetric dichasia of 3-5 flowers; **bracts** tardily deciduous where stipule-like on main stem, early deciduous elsewhere, at first branching point broadly (ob)ovate, 4-12 × 1.4-8 mm, at later branching points ovate, apices acute - rounded, margins usually entire, occasionally fimbriate. **Male flowers: pedicels** 5-14 mm; **tepals** 4, pink, outer pair (sepals) oblong-ovate - broadly ovate, 6-10.8 × 4-6.2(-8.2) mm, apex rounded, margin entire; inner pair (petals) oblanceolate - elliptic, 3.4-6.6 × 1.4-2 mm, apex acute, margin entire; **androecium** very broadly obovoid, becoming obconical with maturity, symmetrical; stamens 14-20; filaments fused basally into a column, 0.4-0.8 mm, the free filaments arising from the upper part of the column, 0.4-0.8(-1.2) mm; anthers oblong-ellipsoid, 0.7-1.2 mm, connective not extended, dehiscing through arcuate slits, eventually down entire length of pollen sacs. **Female flowers: pedicels** 8-19 mm, elongating in fruit; **tepals** 4 (or 3), pink, outer pair (sepals) ovate - broadly ovate, 6.6-11.6 × 5.2-9 mm, apex rounded, margin entire; inner pair (petals) (ob)lanceolate, 3.2-8.4 × 1.5-3.2 mm, apex acute, margin entire; **ovary** obovoid (- ellipsoid), 5-6 × 2-4.8 mm, 3 wings, triangular, 1 longer, extending upwards, 3-locular, placentae axile, bilamellate, bearing numerous minute ovules on both sides; **styles** 3, persistent, briefly fused at base for 0.1-0.6 mm, whole style 1.4-3.0 mm, (capitate -) reniform, becoming lunate when mature, branches 0.4-0.8 mm, a continuous papillose stigmatic band encircling tops of styles. **Capsule** becoming scarious, 15-18 × 7-11 mm, main body obovoid-cordoid, 6-8 × 4.5-7 mm; wings 3, oblong-triangular, 1

longer, 7-13 mm, lower margin ± straight, 10-17.5 mm, upper margins ± horizontal - ascending up to 45°, tip rounded - acute, 0.4-2.8 mm wide distally, wings exceeding capsule 0.4-1.0 mm distally, 1-2 mm proximally; dehiscence at margins of capsule body.

DISTRIBUTION: Southwest Sichuan, in the Muli Kingdom, 2700 - 4300 m and South and West Yunnan, around Kunming, 1800 - 3400 m. See fig. 4.2.

ECOLOGY & BIOLOGY: This subspecies is found growing in moist, shady situations and more open situations. Habitats include moist banks, water courses, shady cliffs and ledges, shady areas of caves, humus covered boulders (at least some limestone), margins of mixed and pine forests, in remnant mixed deciduous, broad-leaved evergreen and coniferous forest and open rocky places in thickets. Plants have been recorded flowering in April, July and October.

DISCUSSION: Irmscher (1939) says that while Rock 5532, 16906 are transitional, "Rock no. 18322 is on the other hand typical **B. holostyla*". I have an isolectotype of this specimen and a photocopy of the US specimen (lectotype) which, unfortunately, does not have any of Irmscher's handwriting on it, sugesting that he did not see this specimen.

ADDITIONAL SPECIMENS EXAMINED: SICHUAN: Mu-Li, shady banks above the Litiang river in wooded valley, 9000 ft, 16.vii.1921, *F. Kingdon-Ward* 4495 (E); Mu-Li, on well shaded limestone rocks in the forest below the cliffs, 9000-10000 ft, 8.viii.21, *F. Kingdon-Ward* 4531 (E); Massif Oua Pao Shan, *M. le. Dr. Legendre* ?438, (P); Kientchang, Lieuming, 2000 ft, 8.ix.1911, *M. le. Dr. Legendre* 1410 (P); **XIZANG (TIBET):** Mekong-Salween, NW of Tsékou, 28° 12' N, 9-10000 ft, Oct. 1904, *G. Forrest* 84 (E); Tsarong, Salween-Kui-chiang divide, 28° 40' N, 98° 15' E, Oct. 1919, *G. Forrest* 19094 (E); Tsarong, Salween-Kui-chiang divide, 28° 40' N, 98° 15' E, Aug. 1919, *G. Forrest* 19277 (E); **YUNNAN:** env. de Yunnan Fan, Mai 1908, native collector comm. M. Yotte, *Ch. d' Alleizette* s.n. (L); environs de Yun-nan-fan, Sept. 1897, *M. Bélard* s.n.

(P); au pied des roches humides sur les haute pics, Août, *M. Bélard* s.n. (P); rochers humides de haute montagnes calcaires, Mt. Pee ngay tze an ? de Ta-pin tze, 4.ix.1882, *M. l'Abbé Delavay* 241 (P) lieux frais et humides de bois quarab.... dans les rochers calcaires humides, Gorges de Santchang Kiou, 27.viii.1884, *M. l'Abbé Delavay* 1230 (P); M. *l'Abbé Delavay* 1895 (L); dans un autre capien, rochers ombragés et humides dessous de Ta-pin-tze, 20.x.1882, *M. l'Abbé Delavay* 4570 (P); Frentes des rochers humides et ombragés, Che tcholzi au dessous de la pin tzi, 2000 m, 16.viii.1888, *M. l'Abbé Delavay* 4570 (P [2]); fentes des rochers humides et ombragés sur le Che-tcho-lze au dessus Jc la pin Jze, 2000 m, 16.viii.1888, *M. Delavay* 4570 (?4970) (E [2]); Yunnan-sen, 1895, *M. l'Abbé Delavay* s.n. (P); environs de Yun-nan-sen, dans les ravins de la montagne, July 1897, *Fr. Ducloux* 452 (P [2]); environs de Lan ?ongry tsiy, plante cueillie par Petrus Py, 9.viii.1904, *Fr. Ducloux* 2614 (P [2]); Eul long kang préfecture de Tchau tong, plante cueillie par le p. M. Mey, 22.vii.1905, *Fr. Ducloux* 4411 (P [2]); Lou pou près Tong Tchouan, *Fr. Ducloux* 6379 (P); Yo lin chan près Tong Tchouan 1910, *Fr. Ducloux* 7307 (P); Mar-li-po, Chung-dzai, 1800-2000 m, 2.xi.1947, *K. M. Feng* 12749 (B); Mekong-Salween divide, 28° 10' N, 10000 ft, Aug. 1917, *G. Forrest* 14682 (E); July 190?, *E. E. Maire* 42? (E); Yun-nan-sen, 1902, *E. E. Maire* 59 (E); rochers de Pan-long-se, 2490 m, Nov. 1914, *E. E. Maire* 374 *pro parte* (E [2],); rochers sous bois-mont. de Song-Tchouan, 2600 m, *E. E. Maire* s.n. (P [2]); Acc. 24/vii/14, *E. E. Maire* s.n. (B); rochers - mont. de Tien-sien, 2800 m, *E. E. Maire* s.n. (P [2]); rochers de Pan-long-se, 2490 m, Oct, *E. E. Maire* s.n. (E); Tali Lichiang Range, grows on the rocks of Ma-Nung mt., 1933, *H. D. McLaren's native collectors* 217 B (BM, E, K); Lo Shuich Mt. (half a mountain), Oct. 1936, *McLaren's collectors* V.89(A) (E [2]); pai-Ching, summit of a mountain, reed. 13.iv.36, *McLaren's collectors* F6 (E); Mt. Wuaha, Yung-ning Territory, 11000 ft, Oct. - Nov. 1932, *J. F. Rock* 24217 (E); Songming Xian, in the vicinity of Longtan, ca. 59 km N of Kunming, 25° 28' N, 102° 46' E, 2100 m, 27.vii.1984, *1984 Sino-Amer. Bot. Exped.* 1337 (E); Kunming Municipality, Xishan, between Taihua and Huating temples, 24° 58' N, 102° 38' E, 2100-2350 m, 31.vii.1984,

Sino-Amer. Bot. Exped. 1541 (E); Chungtien, Lomahua, 2400 m, 11.xi.1937, *T. T. Yü* 10928 (E);

The following specimens were identified as being intermediate between *B. grandis* subsp. *grandis* and *B. grandis* subsp. *holostyla* or *B. asperifolia* Irmsch.. They are included within the circumscription of *B. grandis* subsp. *holostyla.* Irmscher (1939) identified most of these specimens as intermediate.

G. Forrest 84 (E), *G. Forrest* 14682 (E), *G. Forrest* 19094 (E), *G. Forrest* 19277 (E), *M. lc. Dr. Legendre* ?438 (P), *J. F. Rock* 5532 (P isosyntype).

Several *nomina nuda* were discovered during the course of this work but, in accordance with recommendation 30A.1 of the ICBN, these are not mentioned here.

4.5.6 *B. JOSEPHI* A.DC.

PLACE OF PUBLICATION: Ann. Sci. Nat. Bot., sér. IV 11: 126, 1859.

TYPE: India, Khasia, 5-6000 ft, *J. D. Hooker & T. Thomson* 34 (holotype: G-DC, microfiche IDC 15(1): 313, 96!; isotypes: A!, B [2]!, K [4]!, L!).

NOTE: Many authors have spelt the epithet 'josephii' but A. de Candolle spelt the epiphet with a single 'i' and '*josephi*' is an exception to rule 2 ii - Rec. 60C.2 (ICBN).

SYNONYMY:

B. josephi var. ***macrocarpa*** A.DC., Prodr. 15(1): 314, 1864, **synon. nov.**

TYPE: India, Sikkim, 5-7000 ft, Regio temp, *J. D. Hooker* 34 (holotype: K!; isotypes: B!, GH!, K [3]!).

B. picta sensu Wall., 1831, *non* Sm. 1805; C. B. Clarke in Fl. Brit. Ind. 2: 639, 1879.

B. scutata sensu Wall., 1831, Numer. List 3686A, *nomen nudum, non* Wall. *ex* A.DC., 1864; C. B. Clarke in Fl. Brit. Ind. 2: 639, 1879.

B. josephi var. ***minima*** C.B.Clarke 1879, "*josephii*", ***synon. nov.***

TYPE: No material indicated by Clarke (1879) and no herbarium material located with such an identification by Clarke or anyone else.

OTHER PLACES OF PUBLICATION: Clarke (1881) Linn. Soc. J. Bot. 18: 118, fig. 22 a, b; Hara (1966) Fl. E. Himal. 214; Hara (1971) Fl. E. Himal. 2: 84; Hara (1979) Enum. Nep.: 181; Grierson (1991) Fl. Bhutan 2(1): 240-241, Fig. 29 a-d; Kumar & Bhattacharyya (1992) J. Econ. Tax. Bot. 16(3): 567.

DESCRIPTION: Acaulescent or very shortly caulescent tuberous herb up to 50 cm tall. **Bulbils** rarely occurring. **Stem** ± erect, 2-4 mm diam.; internodes up to 12.5 cm;

stipules (late) deciduous, ovate-triangular, 3.2-5 × 2.4-3 mm, apex acute, margin entire or irregularly dentate. **Petiole** green to red, 1.5-32 cm, short, 0.4-0.6 mm and long, c. 2 mm hairs present, increasing towards apex; **leaf blade** green above, variably red below, upper leaf surface sparsely to densely hispid, veins sparsely hirsute, lower leaf surface ± glabrous to pubescent, veins hirsute, ⊥ symmetrical, ovate, 5.5-33 × 4.5-29 cm, leaf base peltate, up to 7 cm deep, apex acuminate, margin up to 5-lobed in the upper two-thirds of leaf blade, lobes with acute to acuminate apices, repand, dentate to denticulate, glandular hairs 0.4-0.6 mm, venation palmate-pinnate of 4-5 main veins, 4-5 veins reaching margin in each half. **Inflorescences** terminal and occasionally axillary asymmetrical dichasial cymes, peduncle up to 23 cm, 40(-100) flowered, male flowers usually maturing first; partial inflorescences slightly asymmetric dichasia, 1-20 flowers, pedicels often appearing compressed for extended period; **bracts** deciduous, glabrous, at first and later branching points not differentiated, linear-lanceolate to ovate, 1.8-5 × 1.6-2 mm, apex acute, margin entire to dentate. **Male flowers: pedicels** 9-12 mm; **tepals** 4, white or pink, outer pair (sepals) ovate to oblong-ovate, 7.2-12 × 3.8-5.5 mm, apex rounded, margin entire, outer surface glabrous or pilose; inner pair (petals) linear-lanceolate, 5-9 × 1.2-2.5 mm, apex rounded, margin entire; **stamens** 11-24, androecium obconical, asymmetrical, filaments fused basally into a column c. 0.2-1.4 mm, free filaments arising from top of column, 0.3-1.2 mm, longer to one side of androecium, anthers oblong to obovate, 1.0-1.8 × 0.5-0.8 mm, connective extended to an obtuse tip, dehiscing through slits down entire length of pollen sacs. **Female flowers: pedicels** 8-12 mm, elongating in fruit; **tepals** 5, white or pink, imbricate, 4 subequal, oblong-ovate, 6-11 × 4.8-7.8 mm, apex obtuse, margin entire; 1 lanceolate, 2.2-7 × 1.6-3 mm, apex acute or rounded, margin entire; **ovary** obovoid-cordate to subglobular-cordate, 2.8-6.4 × 2.8-5.2 mm, glabrous to pilose, 3 wings, triangular, 1 longer, ± horizontal to ascending, 3-locular, placentae axile, bilamellate, bearing numerous minute ovules on both sides; **styles** 3, persistent, variably fused up to half way, whole style 2.4-3.2 mm, reniform, becoming lunate when mature, very rarely, two branched, branches up to 1 mm, a continuous papillose stigmatic band encircling top of styles. **Capsule** becoming

scarious, 10-28 × 6-15 mm; main body obovoid-cordate to subglobular-cordate, 4-10 × 4-8 mm, wings 3, triangular to oblong-triangular, 2 rib-like, 1 longer, 8-22 mm, upper margin ± horizontal to ascending up to 45°, straight to convexally curved, lower margin 9-30 mm, almost straight - slightly repand (to convexally curved), tip acute, occasionally rounded, 1-2.5 mm wide distally, wings exceeding capsule 0.2-0.8 mm distally, 1-3.5 mm proximally; dehiscence at margins of capsule body. **Seeds** oblong-elliptic, c. 0.3 mm.

USES: Stems used in pickles (*teste* KEKE 1015).

DISTRIBUTION: Eastern Nepal, 1800-3700 m; Bhutan, 610-2743 m; India, Sikkim, 1000-2100 m; Darjeeling, 1800-2400 m; Assam, 1524-2438 m; Khasia, 1219-1829 m; North East Upper Burma. See fig. 4.1.

ECOLOGY & BIOLOGY: *B. josephi* is found growing in very shady wet conditions on moss covered rocks, cliffs and shady banks, often buried under shrubs and herbaceous plants. It has been found along roadside cliffs, wooded river banks and deep damp forested gullies, in evergreen *Castanopsis* forest, mixed *Rhododendron* forest and *Quercus semecarpifolia* forest. It is said "to show up well in the dark forest where flowers are conspicuously absent, at least in the very thin undergrowth" (*F. Kingdon-Ward* 3508, E).

DISCUSSION: Neither of the two varieties recognised in the *Fl. Brit. India* has been upheld here. No specimens were found in K, BM or E with any indication of a 'var. *minima*' by C. B. Clarke or any one else. The defining character of *B. josephi* var. *macrocarpa* was said to be long lax hairs on the female capsule but when specimens were examined from the entire distribution of the species, this was found to be a variable character which did not follow any geographic pattern.

ADDITIONAL SPECIMENS EXAMINED: NEPAL: E. Himalaya, Munsong, 5000 ft, 5.x.1940, *K. Biswas* 4402 (GH); Nepal, Taktor, 9-12000 ft, 1930, *Capt. L. Dhwoj* 0400

(BM); Sankhuwasabha District, Arun Valley, ridge between Bhotebas and Chichila, 27° 26' N, 87° 12' E, 1940 m, 20.ix.1991, *EMAK* 84 (E); ibidem, 1950 m, 20.ix.1991, *EMAK* 85 (E); Ridge NE of Guphar Pokhari, 27° 18' N, 87° 33' E, 2865 m, 30.viii.1989, *KEKE* 105 (E); Above Yamphudin, 27° 27' N, 87° 56' E, 1800 m, 27.ix.1989, *KEKE* 1015 (E); Tamur Valley, Walungchung Gola, 8500 ft, 20.vii.1956, *J. D. A. Stainton* 1069 (BM, E); Terhathum, 27° 05' N, 87° 32' E, 7000 ft, 11.ix.1967, *Williams & Stainton* 8455 (BM); **INDIA: SIKKIM:** Penuongchi, 7000 ft, 7.x.1875, *C. B Clarke* 25097A (E); Mongpo, 4000 ft, 1.x.1884, *C. B. Clarke* 36100A (BM); Burting, 3500 ft, 5.x.1875, *C. B. Clarke* 25032F (BM); Barling, 3500 ft, 5.x.1875, *C. B. Clarke* 25032D (E); E. Himalaya, Manibhanjin, 8000 ft, 12.viii.1913, *R. Lepcha* 1222 (E); ex herb. Hort. Bot. Calcuttensis, 1857, *T. Thomson* s.n. (L); **DARJEELING:** Labdah, 5000 ft, 27.ix.1912, *G. H. Cave* s.n. (E); Rongbe, 6000 ft, 20.ix.1917, *G. H. Cave* s.n., (E); 7000 ft, 3.ix.1912, *G. H. Cave* s.n. (A, E); Rungbee, 6000 ft, 17.viii.1869, *C. B. Clarke* 8725 (BM); 7800 ft, 7.viii.1875, *C. B. Clarke* 26878E (BM); 19??, *J. M. Cowan* s.n. (E); 9 km above Mungpoo, 26° 58' N, 88° 19' E, 1900 m, 3.viii.1992, *ESIK* 1076 (E); **BHUTAN:** near Shamgong, 1985, *I. Broad* 305 (E); Mangde Chu Bridge near Tongsa, 27° 30' N, 90° 29' E, 2000 ft, 18.v.1979, *Grierson & Long* 1129 (E); Pang La, 9000 ft, 15.viii.1933, *Ludlow & Sherriff* 466 (BM); Trashiyangsi Valley, 8500 ft, 29.viii.1934, *Ludlow & Sherriff* 906 (E); ibidem, Tobrang, 8500 ft, 29.viii.1934, *Ludlow & Sherriff* 907 (BM [2]); Trashiyangsi, 8000 ft, 9.ix.1934, *Ludlow & Sherriff* 947 (E); Chendebi, 8500 ft, 5.viii.1937, *Ludlow & Sherriff* 3524 (E); Trashiyangse Chu, Sherpang, 6500 ft, 17.viii.1949, *Ludlow, Sherriff & Elliot* 21033 (BM); Between Trashiling and Chendebi, 7500 ft, 6.viii.1949, *Ludlow, Sherriff & Hicks* 17061 (E); Near Chendebi, 8500 ft, 8.viii.1949, *Ludlow, Sherriff & Hicks* 17080 (BM, E); Sherpang (Trashiyangse Chu), 6500 ft, 17.viii.1949, *Ludlow, Sherriff & Hicks* 21033 (E); Thimphu District, Dotena, Thimphu Chu, 27° 35' N, 89° 38' E, 2560 m, 5.ix.1984, *Sinclair & Long* 4850 (E); **ASSAM:** Mts Khasia, zone temp., 1500-1800 m, July 1909, *Ch. d' Alleizette* (L); Thevopesimu Reserve, 6000 ft, 7.viii.1942, *N. L. Bor* 16283 (L); Shillong, Khasia & Jaintia Hills, 5000 ft, 2.x.1953, *N. L. Bor* 18439 (L); Khasia, Sayung, 5000 ft,

12.ix.1886, *C. B. Clarke* 44740B (B); Khasia, Kalipani, 4000 ft, 10.ix.1885, *C. B. Clarke* 40371 (B); Khasia, Mairang, 5000 ft, 12.ix.1886, *C. B. Clarke* 45693C (BM); Laitlyngkot, 5-6000 ft, 17.vii.1946, *F. Kingdon-Ward* 16047 (E); Senge Dzong, 8000 ft, 16.viii.1938, *F. Kingdon-Ward* 14092 (BM, E); Mawphlang, Khasi Hills, 6000 ft, 10.ix.1949, *W. N. Koelz* 23790 (L); **BURMA:** (North East Upper Burma), Rit jawing, 7000 ft, 12.viii.1919, *F. Kingdon-Ward* 3508 (E); **UNKNOWN:** ?India, Soom Forest, 5000 ft, 3.i.1938, *K. Biswas* s.n. (GH); E. Himalaya, *Griffith* 2564 (B, P); E. Himalaya, *Griffith* 2563 (B, P).

4.5.7 *B. LABORDEI* H.LÉV.

PLACE OF PUBLICATION: Bull. Soc. Agric. Sarthe 59: 323, 1904

TYPE: China, Prov. du Kouy-Tchéou, montagnes de Kao-Po, fleurissant sous la pluie d'une cascade dans une avant-grotte, 11.ix.1899, *J. Laborde & E. Bodinier* 1952 bis, (lectotype designated here: B! isolectotype: P!); Prov. du Kouy-Tchéou, sous Pref. de Tchen-lin, à lo-pie, paroci d'une grotte, liges florales partant de la ravine, 8.x.1897, *L. Martin & E. Bodinier* 1952 (syntypes: E! P [3]!).

SYNONYMY:

B. harrowiana Diels, Notes Roy. Bot. Gard. Edinburgh 5: 166, 1912. M. F. Gagnepain, Bull. Mus. Paris 25: 282, 1919 [=*B. labordei*].

TYPE: on the eastern flank of the Lichiang Range, 27° 20' N, 9500-10500 ft, Sept. 1906, *G. Forrest* 3055 (lectotype designated here: E!; isolectotypes: B!, P!); China, Yunnan, at the base of the eastern flank of the Lichiang Range, 27° 10' N, 8500-9000 ft, July 1906, *G. Forrest* 2647 (syntype: E!); SW China / E Tibet, moist shady situations by the sides of streams in the Tali valley 25° 40' N, 6700 ft, June-July 1906, *G. Forrest* 4388 (syntype: E!; isosyntype: BM!); Yunnan, rocky situations in side valleys on the eastern flank of the Tali Range, 25° 40', 7-8000 ft, Aug. 1906, *G. Forrest* 4389 (syntype: E!; isosyntype: B!); SW China / E Tibet, eastern flank of the Tali Range, 25° 40' N, 9000 ft, Sept. 1906, *G. Forrest* 4390 (syntype: E!; isosyntypes: B!, BM!); Yunnan, lieux ombragés et humides à Ta long tan près de Ta pin tze, 17.ix.1888, *Delavay* 3248 (isosyntypes: P [2]!, US!); Yunnan, *Delavay* 3925 (syntype: E; isosyntype: P!); Yunnan, south of Red River from Manpan, 6000 ft, *A. Henry* 9677A (syntype: E!; isosyntypes: B!, US!);

Note: Although Diels differentiated the Forrest specimens from the Delavay and Henry specimens, there was no indication of type status and none are annotated as such, therefore all the specimens cited by Diels are syntypes.

B. polyantha H.Lév., Cat. pl. Yun-Nan: 17, 1915.

TYPE: China, "K. Tchéou B. *sp. nov. polyantha*", handwriting of *J. Cavalérie* s.n. (E - Irmscher writes 'standardum *B. polyantha* Lévl.');

henryi* × *sinensis Irmsch., Mitt. Inst. Allg. Bot. Hamburg, 6: 356, 1927. Irmscher in Handel-Mazzetti (ed.), Symb. Sin. 7: 388, 1931.

DESCRIPTION: Acaulescent to shortly caulescent moliniform rhizomatous herb up to 45 cm tall. **Bulbils** not observed. **Stem** ± erect, occasionally up to 3 cm; **stipules** caducous, ovate-triangular, 2-6 × 0.6-3 mm, apex acute, margin ± entire, occasionally fimbriate. **Petiole** 2-30 × <0.1-0.7 cm, ± glabrous to sparsely pilose or densely hirsute; **leaf blade** red underneath, upper leaf surface ± glabrous or tomentose, lower leaf surface (sparsely) hirsute on veins, slightly asymmetrical, ovate to subrotund, 5.5-19 × 4.5-20 cm, leaf base ± equally cordate, lobes (0.3-)1-4(-6) cm, often overlapping, spreading apart, apex gradually acuminate, margin sometimes shallowly lobed at vein endings, the lobes with acuminate apices, (bi-)crenate-serrate-dentate to denticulate or serrulate, venation palmate-pinnate of 5-6 main veins, 4-6 veins reaching margin in each lobe. **Inflorescence** a terminal asymmetric dichasial cyme, all branches usually on one side of main stem, peduncle up to 22 cm, c. 2-40 flowered, bisexual, male flowers usually maturing first, partial inflorescences slightly asymmetric dichasia, 2-8 flowers; **bracts** caducous, not differentiated, except by size, (broadly ovate -) ovate-triangular to linear-triangular, 1.2-7(-10) × 0.5-3(-8) mm, apex acute to rounded, margin fringed with glandular hairs. **Male flowers: pedicels** 7-11 mm; **tepals** 4, pink or white, outer pair (sepals) ovate, 4.5-10 × 4-7 mm, apex acute (-rounded), margin entire; inner pair (petals) oblanceolate, 5.4-11 × 1-2 mm, apex rounded or acute, margin entire; **stamens** 10-15, androecium obconical, slightly asymmetrical, filaments fused basally into

column, (0.4-)0.6-0.8 mm, the free filaments arising from top of the column, 0.4-0.6 mm; anthers obovoid to ellipsoid, 0.8-1.2 mm, connective not extended, dehiscence through slits down entire length of pollen sacs. **Female flowers: pedicels** 11-15 mm, elongating in fruit; **tepals** 4 (rarely 3), pink or white, valvate; outer pair obovate, 6-8.2 × 4-5.8 mm, apex rounded, margin entire, purple hairs on outer tepal surface; inner pair oblanceolate, 5.4-10 × 1.2-2.2 mm, apex rounded or acute, margin entire, glabrous; **ovary** obovoid-cordate, 3.4-6 × 1-3.8 mm, 3 wings, triangular, 1 longer, upper margin ± horizontal, 3-locular, placentae axile, bilamellate, in at least part of 2 locules, bearing numerous minute ovules on both sides; **styles** 3, persistent, united at base for 0.6-1.5 mm, whole style 1.2-3.6 mm, reniform, becoming lunate when mature, branches c. 0.2 mm, with a continuous papillose stigmatic band encircling top of style. **Capsule** becoming scarious, 7-10.5 × 13-21 mm, main body, obovoid-cordate to obovoid-ellipsoid, 5-7 × 5-5.2 mm; wings 3, triangular, 1 longer, 11-17 mm, upper margin sinuate - convexly curved, lower margin sigmoid, 13-26 mm, upper margin ± horizontal - ascending up to 30° (-60°), tip acute, 0.6 mm wide distally, wings exceeding capsule 0.4-1.2 mm distally, 0.8-2.5 mm proximally; dehiscence at the margins of the capsule body.

DISTRIBUTION: China, S Sichuan near Yungning, 2700 - 3000 m; NW Yunnan, around Lijiang up to c. 3400 m, Central Yunnan, in the Western Hills near Kunming, SW Yunnan, around Simao, c. 1200 - 1500 m and SE Yunnan, around Wen-shan-hsien and Mengzi, 1800 - 2200 m; Guizhou - localities not determined; Burma, around the border with Yunnan at Sadou, 25° 22' N 97° 53' E, Fenshuiling Hkyet Pass (Fen-shui-ling-ya K'ou - China) 25° 49' N, 98° 40' E, 2000 - 2500 m, and Hpimaw Hkyet (P'ien-ma-ya K'ou - China), 26° N, 98° 40' E, 3000 m; North Vietnam, near Tonkin, Chapa, 1600 m. See fig. 4.1.

ECOLOGY & BIOLOGY: This species is found growing in wooded, shady, humid situations; by mountain streams; on mossy cliff faces and moss covered boulders; in

cracks in rocks; by waterfalls; in mixed (including *Quercus*) temperate forests and the "upper" rain forest; on substrate recorded as calcareous or schist.

ADDITIONAL SPECIMENS EXAMINED: CHINA: GUIZHOU (KOUY-TCHÉOU): District de Triu-gon(?), Kao-Peo, grottes, Chutes d'eau, *J. Cavalérie* 1165 (E); gan chouen grottes, *J. Cavalérie* 3878 (P); 1918, *J. Cavalérie* 4120 (P); *J. Cavalérie* s.n. (P[2]); Kao-Peo, July 1903, *Cavalérie & Fortunat* 1165 (P); route Conan-Po, Pui-Pu, 18.viii.1905, *Cavalérie & Fortunat* 2445 (P); Route Imperiale entre Pui-ue et Koui-tui près d'une chute d'eau sur haut de la roche, 18.viii.1905, *Cavalérie & Fortunat* 2500 (P); Tchong Thong (grottes), 1300 m, April 1914, *M. Esquirol* 5047 (P); **YUNNAN:** lieux humides des bois - les gorges de Gan tchang Kion (Flo Kin) sur la route de Toc - li à Hu Kin, bep....?, 27.viii.1884, *Delavay* 1229 (P); lieux humides et ombragés sur le che teho tze au dessou de ta pin tze, 2000 m, 27.viii.1885, *Delavay* 2597 (P[2]); au pied du Mt.-Yong in ? dans les gorges du Yang in ? près de Lan Kong, 7.viii.1883, *Delavay* s.n. (P); environs de Yun-nan-sen, montagnes - fissures des rochers, 10.viii.1904, *F. Ducloux* 2615 (P); Yun-nan-sen, le ching chan ravines, 8.viii.1905, *F. Ducloux* 3607 (P); Kou ty Region de Pin tchouan, plante cueillie par Jean Py, 1911, *F. Ducloux* 7060 (P); environs de Yunnan-sen, montagnes, fissures de rochers, 10.viii.1904, *F. Ducloux* s.n. (E); Wen-shan-hsien, Lao Chun shan, 1800-2200 m, 12.viii.47, *K. M Feng* 11116 (B); Wen-shan-hsien, Mao-luh-tarng, 2000-2200 m, 17.viii.1947, *K. M. Feng* 11319 (B); *G. Forrest* 6413 (P); 1930-31, *G. Forrest* 28974 (BM, E); Mengtsz, 6-7000 ft, Dec. 1894, *W. Hancock* 260 (K); prope urbem Lidjiang ("Likiang"), imprimis in monte Yulung-schan, leg. VI-XI, 1914, 1915, 1916 collectores indigeni (Diar. Nr. 661, 1182, 1206, 1681, 1901), *H. F. v. Handel-Mazzetti* 3728 (WU); in pluvii silvis mixtis temperatis supra vicum Bahan (Pehalo) ad fluvium Lu-djiang (Salween), 27° 58' N, 2700 m, 23.viii.1916, *H. F. v. Handel-Mazzetti* (Diar. Nr. 1858) 9940 (B, WU); Mengtze, east mountains, 6000 ft, *A. Henry* 9677 (BM, E); Szemao, 5000 ft, *A. Henry* 12505 (E, K); Szemau, 4500 ft, *A. Henry* 12645 (B, E, US); Fu-?sh, 5000 ft, *A. Henry* 13266 (B, E, US); Teng-yueh, *E. B. Howell* 127 (K); Yun-nan-sen vicinity, *E. E. Maire* 2341 (K); Lichiang

Range, 1933, *H. D. McLaren's native collectors* 128L (BM); Yangtze watershed, Prefectural District of Likiang, eastern slopes of the Likiang snow range, Peshive River, among rocks, 11000 ft, 1.viii.1922, *J. F. Rock* 5274 (US); Yangtze watershed, western slopes of Likiang snow range, among boulders, July 1922, *J. F. Rock* 5385 (BM, P, US); west of Talifu, Mekong watershed, en route to Youngchang and Tengyueh, Sept-Oct 1922, *J. F. Rock* 6605 (B, US); eastern slopes of the Likiang snow range (Yu-lung shan), Mt. Satseto, on boulders, 11000 ft, June-August 1932, *J. F. Rock* 24901 (BM); ibidem, June-August 1932, *J. F. Rock* 24928 (K, US); in reg. Lichiang, prope ? Reh, 3000 m, 31.vii.1914, *C. Schneider* 2098 (B, K, US); in valle flume Salween versus Tai pingpen, 1800 m, Oct. 1914, *C. Schneider* 2567 (B, K); Taron-Taru Divide, Lahpi, 1900 m, 26.viii.1938, *T. T. Yü* 19935, (E); **SICHUAN:** SE of Yungning, 27° 36' N, 100° 48' E, 9-10000 ft, Sept. 1922, *G. Forrest* 22416 (P, US); **UNKNOWN:** "*B. labordei* Lévl. et Vant, rochers humides août 1905" (E); **BURMA:** Fen Shui Ling Valley etc., on mossy cliff-faces etc. in the upper rain forest, 7-8000 ft, 9.ix.1919, *R. Farrer* 1305 (E); descent of the Sanse gorge to Sadou, 25° 25', Sept. 1912, *G. Forrest* 9125 (E); Hpimaw pass, N Maikha - Salwin divide, 26° N, 98°40' E, 10000 ft, Aug. 1924, *G. Forrest* 24835 (E); **NORTH VIETNAM:** Tonkin, Chapa, Massif du Song ta Van, vers 1600 m, Aug. 1936, *Petelot* 7.086 (B [2]).

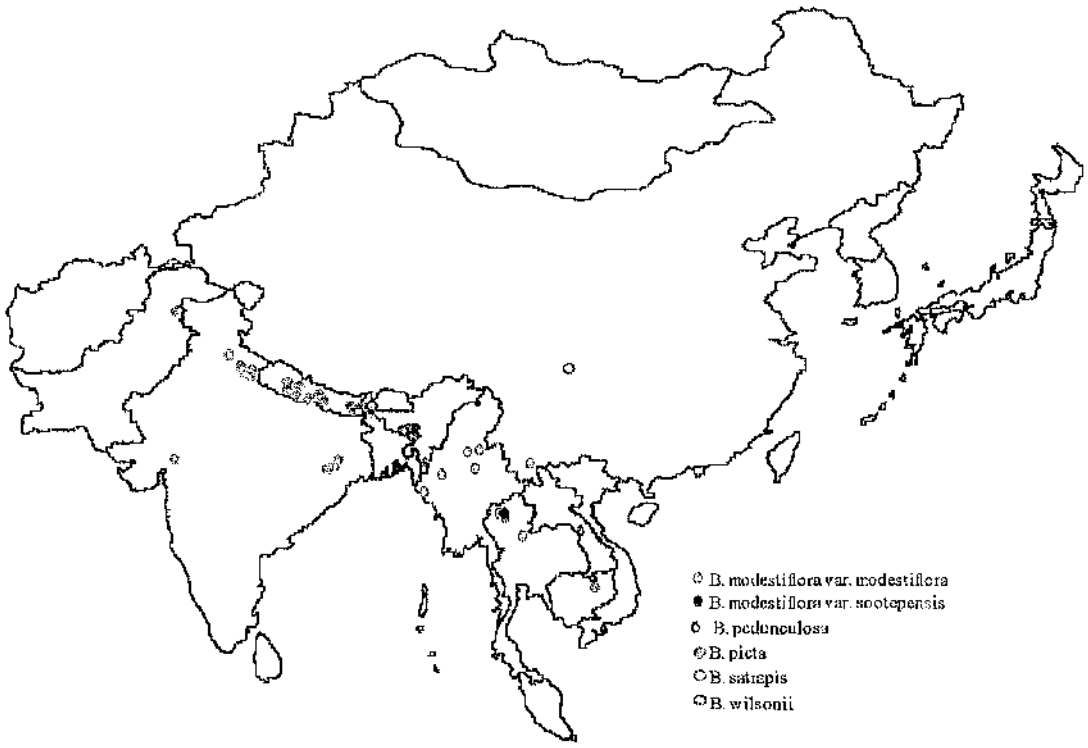


FIG. 4.3 MAP TO SHOW DISTRIBUTION OF *B. MODESTIFLORA*, *B. PEDUNCULOSA*, *B. PICTA*, *B. SATRAPIS* AND *B. WILSONII*

4.5.8 *B. MODESTIFLORA* KURZ

PLACE OF PUBLICATION: Flora, 54 (18):296, 1871

TYPE: Burma, Arracan, Boronga Island, in evergreen forest on sandstone rocks, October 1869, *Kurz s.n.* (holotype: K!; isotype: K!)

SYNONYMY:

B. yunnanensis H.Lév., Repert. Spec. Nov. Regni Veg. 7: 20 (1909) **synon. nov.**

TYPE: China, Yunnan, Szemao, W. mts., 5000 ft, *A. Henry* 12403C, (holotype: E!; isotypes: B!, BM!, HBG!, K!, L!).

B. yunnanensis var. ***hypoleuca*** H.Lév., Cat. pl. Yun-Nan 17, 1915, *nomen nudum*; Golding & Karegeannes in L. B. Smith *et al.*, Smithsonian Contr. Bot. 60: 251, 1986.

B. sootepensis var. ***thorelii*** Gapnep., in Lecomte, Fl. Indo-Chine 2(8): 1104, 1921 **synon. nov.**

TYPE: Laos, Expédition du Me-Kong, Bassac, 1866-1868, *M. le Dr. Thorel* s.n., (lectotype designated here: P!); île Khon, *M. le Dr. Thorel* 2226 (syntype: P!; isosyntype: K!); île Khon, *M. le Dr. Thorel* 2239 (syntype: P!; isosyntypes: BM!, E!);

B. lushaiensis C.E.C.Fisch., Bull. Misc. Inform. 121: 273-274, 1928 **synon. nov.**

TYPE: India, Assam, Lushai Hills, Sialsuk, 4-5000 ft, July 1926, *A. D. Parry* 39 (holotype: K!).

B. yunnanensis var. ***thorelii*** (Gagnep.) Golding & Kareg., Phytologia 54(7): 499, 1984 **synon. nov.**

OTHER PLACES OF PUBLICATION: Clarke (1879) in J. D. Hooker, Fl. Brit. Ind. 2: 640, 1879 *pro parte*; Clarke (1881) J. Linn. Soc. 18: 118, fig. 25; Gagnepain (1921) Fl. Indo-Chine 2(8): 1103

DESCRIPTION: Caulescent, fibrously rooted - tuberous herb up to c. 50 cm tall. **Bulbils** present in nodes of stem and root. **Stem** erect, occasionally procumbent, up to 6 mm diam.; internodes up to 17 cm, ± glabrous to hirsute (to densely hirsute); **stipules** deciduous, lanceolate to oblong-ovate, 2-10.8 × 0.6-6.4 mm, apex acute to acuminate, margin serrate-fimbriate, ± glabrous to hirsute. **Petiole** 0.5-12.5 cm, sparsely hairy, increasing towards apex; **leaf blade** upper surface sparsely to densely tomentose, lower surface veins (sparsely) hirsute, very rarely with stellate hairs, asymmetrical, (broadly ovate to) ovate-triangular, (0.7-)2.4-12.5 × (0.3-)1.2-8 cm, leaf base unequally cordate, lobes 0.2-2.6 cm deep, diverging (rarely parallel), apex acute to acuminate (to very acuminate), margin tending to repand, (bi)dentate to (bi)denticulate, largest teeth at vein endings; venation palmate-pinnate of 3-4 main veins, 2-3 veins reaching margin in small lobe, 4-5 in large lobe. **Inflorescence** a terminal raceme, 2-25(-37) cm, 2-44 flowered, bisexual, male or female flowers maturing first; partial inflorescences ± symmetrical dichasia, 2-4 flowers, up to 8 "unbranched dichotomies"; **bracts** usually tardily deciduous (rarely caducous), oblong-(ob)ovate to lanceolate, 3.4-12 × 1.2-4 mm, apex acute or rounded, margin dentate-fimbriate where stipule-like, subtending partial inflorescences; tardily deciduous, ovate, 1-4.5 × 0.2-1 mm, apex acute, margin fimbriate elsewhere. **Male flowers: pedicels** 6-18 mm; **tepals** 4, pink or more rarely white; outer pair oblong-ovate to broadly ovate, 3.6-10 × 2-8.8 mm, apex acute, margin entire, (glabrous to) setulose; inner pair lanceolate to linear-lanceolate, 1-4.4 × 0.4-1.6 mm, apex acute, margin entire, glabrous; **androecium** obovoid to obconical, slightly asymmetrical; stamens 12-24; filaments fused basally into a column 0.2-1.0 mm, the free filaments arising from the top of the column, 0.4-1.0 mm; anthers obovoid (to oblong), 0.8-1.2 × 0.4-0.6 mm, connective extended into an ovate tip, dehiscing through slits eventually down entire length of pollen sacs. **Female flowers: pedicels** 11-23 mm,

elongating in fruit; **tepals** 5, pink, 4 subequal, lanceolate - ovate, 3.6-10.4 × 2-7 mm. apex acute - rounded, margin entire, ± glabrous; 5th tepal, linear-lanceolate, 2.5-6.6 × 0.8-1.5 mm, apex acute, margin entire; **ovary** obovoid - ellipsoid, 3-7 × 2-4 mm, 3 wings, triangular, 1 longer, ± horizontal, 3-locular, placentae axile, bilamellate, bearing numerous minute ovules on both sides; styles 3, decidous, briefly fused at base for 0.2-0.8 mm, whole style 2.2-4 mm, lunate, branches 0.6-0.8 mm, a continuous papillose stigmatic band encircling tops of styles. **Capsule** becoming scarious, 10-34 × 8-19 mm, main body ellipsoid - obovoid, 6.6-10.5 × 4.2-7 mm; wings 3, 1 longer, 6-28 mm, lower margin straight to elliptically curved or sigmoid, 10-32 mm, upper margins ± horizontal or ascending up to 30°, tip acute or obtuse, 1-3 mm wide distally, wings exceeding capsule 1-2 mm distally, 1.5-4 mm proximally; dehiscence at margins of capsule body.

DISTRIBUTION: India, Assam, Lushai Hills; Burma, Akyab, Arakan, Mt. Victoria region and North Shan State; China, SW Yunnan, Szemao; Laos; Thailand, Pâyap. See fig. 4.3.

VERNACULAR NAMES: In Assam, India the native name is Seikhupthurata (*teste A. D. Parry* 39), while in Northern Thailand it is known as Som Koung (*teste J. E. Vidal* 5241).

USES: The leaves of the species are used in soups to aid digestion (alimentaire) (teste *J. E. Vidal* 5241).

ECOLOGY & BIOLOGY: *B. modestiflora* will grow in shade, on vertical limestone or sandstone rock (may be south facing) and on shale or granite bedrock. It has been found growing along the soil embankments of seasonal and permanent streams in evergreen or deciduous forest with teak and bamboo in rich soil or crevices of wet rock. It has been noted in fire-prone areas (*teste J. F. Maxwell* 93-1090).

DISCUSSION: This is a very variable species and the status of *J. F. Maxwell 89-1151*, *J. F. Maxwell* 91-879 and *L. Vanpruk* 339 cannot be confirmed without field work. These specimens have many unbranched dichotomies in the inflorescences characteristic of

section *Parvibegonia* and caducous stipule-bracts in the terminal inflorescence. These differences are not geographically based and may be a reflection of poor environmental conditions.

ADDITIONAL SPECIMENS EXAMINED: INDIA: ASSAM: Lushai Hills, Sialsuk, 4-5000 ft, Sept. 1927, *A. D. Parry* 39 (K [2]); **BURMA (MYANMAR):** Bhamo, 10.ix.1868, *D. J. Anderson s.n.* (K); Mindat, 4000 ft, 6.vii.1956, *F. Kingdon-Ward* 22460 (GB [2]); Southern Chin Hills, Mt. Victoria region, Esakan, 6000 ft, 6.ix.1956, *F. Kingdon-Ward* 22680 (GB [2]); North Shan States, Gokteik Gorge, 1500 ft, 2.viii.1908, *J. H. Lace* 4159 (A, E, K *pro parte*); North Shan States, Gokteik District, 2100 ft, 7.x.1911, *J. H. Lace* 5448 (E, K); Upper Chindwin District, opposite Kindat, 24.viii.1908, *J. H. Lace* s.n. (K); Moulmein, 1862, *Parish 11* (K); Katha District, Pilo Reserve, Gyodaung - Ziyatin Forest Rest House, 800 ft, 21.viii.15, *C. G. Rogers* 993, (E); **CHINA: YUNNAN:** Szemao, W. mts., 4000 ft, *A. Henry* 12403, (K); Szemao, W. mts., 4500 ft, *A. Henry* 12403A (K, B); Szemao, W. mts., 5500 ft, *A. Henry* 12403D, (B, E, BM, E, K, MO); Szemao, W. mts., 5000 ft, *A. Henry* 13482, (B, E, K, MO); **LAOS:** fôrets près Luang Brabury, 1903, *Joseph por Ch. d' Alleizette* s.n. (L); Expédition du Me-Kong, Stung-streng, 1866-1868, *M. le Dr. Thorel* 2239 (P [2]); **THAILAND (SIAM):** Doi Chieng Dao, steep slope SW of Ban Tam, c. 730 m, 15.viii.35, *H. B. G. Garrett* 976 (K); Doi Sutep, 600 m, 26.viii.11, *A. F. G. Kerr* 1970 (BM, E *pro parte*, K); Doi Sutep, 1500 ft, 23.xi.1912, *A. F. G. Kerr* s.n. (ABD); Chiang Mai, Muang, Doi Sutep, east side, Kohntatahn Falls, 600 m, 4.xi.1987, *J. F. Maxwell* 87-1363 (L); Chiang Mai, Muang, Doi Sutep, east side of Chang Kian valley, 1025 m, 23.viii.1988, *J. F. Maxwell* 88-1033 (L); Chiang Mai, Mae Rim, Doi Sutep-Pui National Park, north side of Mae Sa Falls, 400 m, 28.ix.89, *J. F. Maxwell 89-1151* (A, E, L, MO); Prae, Song, Mae Yom Nati National Park, Dow Boon Subdistrict, west side of Yom River, opposite Huey Lie Station area, 225 m, 11.x.1991, *J. F. Maxwell* 91-879 (E, GH, P); Lampoon, Mae Tah, Doi Kuhn Dahn National Park, along the trail to Mah Meun Station, 1000 m, 24.ix.1993, *J. F. Maxwell* 93-1090 (L); Chiang mai, Lampoon, Mae Tah Muang, Doi

Sutep-Pui National Park, east side below Sahn Goo ruins, 1500 m, 16.ix.1993, *P. Palee* 156 (L); Payap, Doi Chiengdao, 12.x.1926, *Put* 304 (ABD); Payap, Doi Chiengdao, 14.x.1926, *Put* 331 (ABD, K); ibidem, 1100 m, 15.vii.1958, *Sørensen, Larsen & Hansen* 4081 (GB); Chiengmai, Doi Sutep, 1000 m, 5.ix.1958, *Sørensen, Larsen & Hansen* 4750 (GB); ibidem, 1000 m, 5.ix.1958, *Sørensen, Larsen & Hansen* 4759 (GB); ibidem, 750 m, 18.ix.1958, *Sørensen, Larsen & Hansen* 5092 (GB); ibidem, 900 m, 18.ix.1958, *Sørensen, Larsen & Hansen* 5096 (GB); Chiang Mai, higher elevation of Doi Chiang Dao, 1100-1800 m, 13.ix.1967, *Tagawa, Shimizu, Hutoh, Koyama & Nalampoon* T9889 (L, P); Prae, Nartan, 800 ft, 22.ix.12, *L. Vanpruk* 339 (K); Chiang Mai, Doi Chiang Dao, 27.ix.1971, *J. E. Vidal* 5241 (P).

4.5.8.1 *B. MODESTIFLORA* VAR. *SOOTEPENSIS* (CRAIB) Z. BADCOCK COMB. NOV.

TYPE: Thailand, Doi Sootep, Chiengmai, 4500 ft, 5.ix.09, *A. F. G. Kerr* 785 (holotype: K!; isotypes: B!, BM!, E!);

B. sootepensis Craib, Bull. Misc. Inform. 57-58, 1911

B. yunnanensis var. ***sootepensis*** (Craib) Craib, Contr. Fl. Siam in Aberdeen. Univ. Studies 57: 95, 1912.

OTHER PLACES OF PUBLICATION: Craib (1931) Fl. Siam. Enum., Siam. Soc., Bangkok p. 780

DIFFERS FROM THE TYPICAL VARIETY BY: **Internodes** up to 10.5 cm; stipules 2.8-10 × 1.2-3.6 mm; **petioles** short, 0.5-8 cm; **leaf blade** upper surface tomentose, hairs 0.5-0.8 mm, 7-57 × 3-20 mm, base of leaf lobes 2-12 mm, leaf tending to dry dark brown.

DISTRIBUTION: Thailand, Pâyap. See fig. 4.3.

ECOLOGY & BIOLOGY: In crevices on damp (granite) rocks in primary evergreen forest and on grassy slopes in pine-forest.

Additional specimens examined: Thailand (Siam): Doi Angka, Doi Pa Mawn spur, south rock face, 1520-1570 m, 20.ix.1927, *H. B. G. Garrett* 457 (ABD, B, E, K, L [2]); Chiengmai, Doi Sootep, 2400 ft, 25.ix.1910, *A. F. G. Kerr* 1420 (B, BM, E, L, P); Doi Sutep, 2000 ft, 26.viii.1911, *A. F. G. Kerr* 1970 *pro parte* (E); Chiangmai, Mai Rim, Doi Sutep, NE side, Ban Mae Sah Mai 12, Huay Mae Nai, 1200 m, 17.viii.1988, *J. F. Maxwell* 88-1010 (L); Chiengmai, Doi Sutep, 1320 m, 31.viii.1958, *Sørensen, Larsen & Hansen* 4645 (GB); Chiengmai, Doi Sutep, 900 m, 18.ix.1958, *Sørensen, Larsen & Hansen* 5096 (L).

4.5.9 *B. PEDUNCULOSA* WALL.

PLACE OF PUBLICATION: Pl. Asiat. rar., 1:82, t. 97, 1830

TYPE: "3672 *Begonia pedunculosa* Wall. A. Mont. Sillet, M. R. Smith", Wall. Num. List 129, no. 3672A (holotype: K-W!; isotype: G!, K!).

NOTE: Wallich (1830) cites the following: "Habitat in montibus prope Sillet, supra saxa, florens sub pluviis, mensibus Junii-Septembris, fructifera Septembri et Octobri. In Hortum Botanicum Calcuttae anno 1817 introduxit M.R. Smith."

MISAPPLIED NAMES:

B. pedunculosa sensu Wall., Numer. List 129, no. 3672B, 1831, *non* Wall., 1830; C.B.Clarke in J. D. Hooker, Fl. Brit. Ind., 2:656, 1879 [=*B. khasiana* C.B.Clarke]; J. Golding, Phytologia, 40:8, 1978 [=*B. khasiana* C.B.Clarke].

B. pedunculosa sensu Grierson, in A. J. C. Grierson & D. G. Long (eds.), Fl. Bhutan, 2(1): 243, 1992, non Wall.

OTHER PLACES OF PUBLICATION: A. de Candolle (1864) Prodr. 15(1): 314; Clarke (1879) in J.D. Hooker, Fl. Brit. Ind., 2:639; Clarke (1881) J. Linn. Soc. Bot. 18: 118, t. II, fig. 23; Smith *et al.* (1986), Smithsonian Contributions to Botany, 60: 212, fig. 27.34.

DESCRIPTION: Caulescent tuberous herb up to 35 cm tall. **Bulbils** sometimes present in upper nodes. **Stem** red-brown, erect; internodes 0.5-6.5 cm, sparsely pilose; **stipules** deciduous, ovate-triangular, 2-5.4 × 0.8-3.2 mm, apex acute, margin (denticulate-)fimbriate. **Petioles** (3-)10-38(-46) mm, pilose; **leaf blade** upper surface (densely) pilose, lower surface veins densely pilose, hairs reddish-brown, up to 1.4 mm, asymmetrical, ovate-oblong, 5.4-9.5 × 2.2-5.5 cm, leaf base unequally cordate, lobes 3-5 and 3-17 mm deep, apex acute, margin coarsely biserrate to dentate with glandular, articulate hairs up to 0.6 mm, venation pinnate of 3 main veins, 3-6 reaching margin in

small lobe, 6-10 in large lobe. **Inflorescences** terminal and axillary racemes, usually bisexual, up to 7 cm, male or female flowers maturing first, 30 flowers, partial inflorescences dichotomous cymes, 1-6 flowers; **bracts** persistent, not differentiated, ovate to oblong-ovate, 1.6-4 × 0.8-2.2 mm, apex acute, margin ± entire. **Male Flowers: pedicels** (4-)9-17 mm; **tepals** 4, pink; outer pair (sepals) broadly obovate to elliptic, 4.2-7.2 × 3.8-5.6 mm, apex rounded, margin entire; inner pair (petals) obovate-oblong, 3.6-5.6 × 1.2-3 mm, apex rounded, margin entire; **androecium** obconical, asymmetrical; stamens 10-18; filaments fused basally into a column up to 0.6-1.2 mm, the free filaments arising from the upper part of the column, 0.4-1.0 mm; anthers obovate-oblong, 0.6-0.8 mm, connective not extended, dehiscence through short arcuate slits. **Female flowers: pedicels** 11-18 mm, elongating in fruit; **tepals** 5, pink, persistent, 4 subequal, broadly ovate to obovate-oblong, 3-6 × 2.2-3.2 mm, apex rounded, margin entire; 5th tepal narrowly elliptic 3.2-5.6 × 1.2-2.2 mm, apex rounded, margin entire; **ovary** obovoid-cordate to subglobular, 3.2-4.8 × 2-4.2 mm, 3 wings, elliptic-triangular, upper margins extending upwards, 3 locular, placentae axile, bilamellate, bearing numerous, minute ovules on both sides; **styles** 3, persistent, briefly fused at base for 0.2-0.8 mm, whole style 1.6-2.8 mm long, lunate, branches 0.2-0.4 mm, a continuous papillose stigmatic band encircling tops of styles. **Capsule** becoming scarious, 13-20 × 8-19 mm, main body ellipsoid, 4-7 × 4-6 mm; wings 3, 1 longer, 9-14 mm, upper margin straight to ascending up to 60°, lower margin elliptically curved, 14-20 mm, tip rounded or acute, 0.6-2.6 mm wide distally, wings exceeding capsule 0.2-0.8 mm distally, 1-2.2 mm proximally; dehiscence at margins of capsule body.

DISTRIBUTION: India, Assam, Khasi Hills, 850 - 1850 m; Bangladesh, Khasi Hills. See fig. 4.3.

ECOLOGY & BIOLOGY: Forms colonies in damp shady places, on cliff faces in dark forest.

DISCUSSION: The type of *B. khasiana* C.B.Clarke was checked in K-W and was not found to be allied to *B. pedunculosa*.

ADDITIONAL SPECIMENS EXAMINED: INDIA: ASSAM: KHASI: Mawphlang, 6000 ft, 21.viii.1952, *Thakur Rup Chand* 6436 (L); Mawphlang, 6000 ft, 24.viii.1954, *Thakur Rup Chand* 8042 (L); Cherra Plateau, 4500-5500 ft, 28.ix.1868, *C.B. Clarke* 5141 (BM); Darain, Jaintia, alt. 4000 ft., 20.xi.1872, *C.B. Clarke* 18328 (E); Mairing, 5000 ft, 30.x.1872, *C.B. Clarke* 19154A (BM); Surareen, alt. 5000 ft, 12.ix.1885, *C.B.Clarke* 40403 (G); Surareen, alt. 5000 ft, 12.ix.1885, *C.B. Clarke* 40438D (B); Shillong, alt. 5500 ft, 24.viii.1886, *C.B. Clarke* 44668B (B); Mausmai, 3750 ft, 23.ix.1886, *C.B. Clarke* 45100 (BM); Vale of Rocks, 5000 ft, 21.ix.1886, *C.B. Clarke* 45452B (G); Surareen, alt. 5000 ft, 22.ix.1886, *C.B. Clarke* 45578A (G); Shillong, alt. 5000 ft, 16.ix.1886, *C.B. Clarke* 47763 (G); alt. 4000-6000 ft, *Griffith* 468 (GH); Regio temp, 4-6000 ft, *J. D. Hooker & T. Thomson* s.n. (B, B - klepto from M no. 159, BM, E, G [2], GH, HBG - klepto from WU, K [2], L [2], P [2]); Cherrapunji, 4000 ft & under, 28.vii.1946, *F. Kingdon-Ward* 16026 (BM); Mawphlang, 5500 ft, 8.vii.49, *F. Kingdon-Ward* 18728 (BM); Mawryngkneng, 4000 ft, 24.ix.1951, *W. N. Koelz* 28599 (L); Mawryngkneng, 4000 ft, 18.x.1951, *W. N. Koelz* 28882 (L); Mawphlang, 6000 ft, 18.viii.1952, *W. N. Koelz* 31154 (L); *sine loc. J. Lobb* s.n. (K); *sine loc. Wm. Mackay* s.n. (K); Tšerapúndzi near Máirong, 2800-4500 ft, 1-30.x.1855, *Herb. Schlagintweit s.n.* (BM); locality of Tšerapúndzi [Cherrapunji] near Máirong, alt. 2800 - 4500 ft, 1-30.x.1855, *Herb. Schlagintweit from India and High Asia, Gen. No. of Catalogue* 256 (B); **BANGLADESH (East Bengal):** herb. EIC 2574, *Griffith* s.n. (B, B - klepto from M, GH, L, P *pro parte*);

4.5.10 *B. PICTA* SM.

PLACE OF PUBLICATION: Exot. Bot. 2: 81, t. 101, 1805

TYPE: Simbu, 21 July 1802, *Buchanan-Hamilton* s.n. (holotype: BM!).

SYNONYMY:

B. hirta Wall. mss. *ex* W. J. Hooker, Exotic Flora. 2:89, 1825, *pro syn. B. picta* Sm., 1805 (NB cited as 1807 by Hooker and not 1805)

B. echinata Royle, Ill. bot. Himal. Mts. 313, t. 80: fig. 1, 1839; A. de Candolle, Prodr. 15(1): 312, 1864.

TYPE: Wall. Ic. ined. 1199 (syntype: K); *G. Govan* 741 (syntype: not located, possibly in DD).

Note: Article 9.14 of the ICBN (1994) allows the typification of a name by an unpublished illustration so long as the institution housing the illustration is stated.

B. erosa Wall. ex C.B. Clarke in J. D. Hooker, Fl. Brit. Ind. 2: 638, 1879, *pro parte*, *non* Blume, 1827; Hara in Enum. Nep. 2:182, 1979.

TYPE: "*Begonia erosa* Wall. Nepalia 1821", Wall. Num. List 129 no. 3688, *pro parte* (holotype: K-W!)

B. rex auct. *non* Putz., Liv. Him. Flow. t. 183, 1964; Hara in Enum. Nep., 2:182, 1979.

OTHER PLACES OF PUBLICATION: Don (1825) Prodr. Fl. Nep. 223; Lodd. Bot. Cab. t. 571, 1821; Hooker (1825) Exotic Flora 2: t. 89; Hooker (1830) Bot. Mag., 57: t. 2962; Wallich (1831), Numer. List 129, no. 3685B and part of A; Kitamura (1955) in F. & Fl. Nep. Him. 183; Liv. Him. Flow. t. 184, 1964; Schilling, J. Roy. Hort. Soc. 94: 222-232, t. 105, 1969; Hara in Fl. E. Him. 215, 1966; 2: 84, 1971; Ghazanfar & Aziz, Flora of

West Pakistan 96: 1-4, 1976; Smith *et al.* (1986), Smithsonian Contr. Bot. 60: 215, fig. 12.3 (icon).

DESCRIPTION: Acaulescent - caulescent tuberous herb up to 50 cm tall. **Bulbils** not observed. **Stem** erect, up to 5 mm diam.; internodes up to 13 cm; **stipules** tardily deciduous, ovate to lanceolate, 2-7 × 1-2 mm, apex acute to acuminate, margin serrulate-fimbriate, hirsute. **Petiole** 2-17 × 0.1-0.5 cm, sparsely hairy; **leaf blade** often colourfully variegated, upper surface ± glabrous to tomentose, hairs 0.2-1.5 mm, lower surface veins sparsely hirsute, ± symmetrical, ovate-triangular to broadly ovate, 4-23.5 × 3.4-16.5 cm, leaf base = equally cordate, lobes 0.6-3.7 cm deep, sometimes overlapping, apex acuminate, margin rarely up to 3-lobed, variably (bi-)serrate to dentate with hairs up to 1 mm, largest teeth at vein endings, venation palmate-pinnate of 3-5 main veins, c. 4-7 in each lobe. **Inflorescence** a terminal dichotomous cyme, peduncle up to 16.5 cm, up to 11 flowered, usually bisexual, male or female flowers maturing first; **bracts** tardily deciduous, not differentiated except by size, ovate to broadly ovate, 1.8-6 × 0.8-3.4 mm and 5-10.2 × 1.6-6 mm, apices acuminate, margin dentate-fimbriate, hirsute. **Male flowers: pedicels** 15-25 mm; **tepals** 4, pink or white; outer pair (sepals) ovate to obovate (9-)14-19 × 9-14 mm, apex rounded to acute, margin entire to serrulate, outer surface with purplish (or white) simple hairs up to 0.8 mm; inner pair (petals) lanceolate to obovate, (6-)8-14 × 5-6 mm, apex acute or rounded (to truncate), margin entire, glabrous; **androecium** oblong-obovate, ± symmetrical; stamens 37-60; filaments fused into a column, 0.7-1.2 mm, the free filaments arising all the way up, 0.4-1.4 (-2.3) mm; anthers oblong-obovate, 0.8-1.4 mm, connective extended into a short ovate tip, dehiscing through slits down entire length of pollen sacs. **Female flowers: pedicels** 8-20 mm, elongating in fruit; **tepals** 5, pink or white, 4 subequal, oblong-ovate, 8-13(-23) mm × 5.4-7.4(-16) mm, apex acute or rounded, margin serrulate-fimbriate, outer surface with purplish (or white) hairs; 5th tepal oblong-ovate, 6.4-7.5 × 3.4-4.4 mm, apex rounded or truncate, margin ± entire, outer surface sparsely hairy; **ovary** subglobular to obovoid, 3-7 × 3-7 mm, 3-wings,

triangular, ± equal to 1 longer, extending upwards, very rarely 2-locular, usually 3-locular; placentae axile, bilamellate, bearing numerous minute ovules on both sides, variably covered in red or white branching (- entire) scales; **styles** 3, persistent, briefly fused at base for 0.4-0.6 mm, whole style 1.9-2.4 mm, bifid, the branches ± erect, c. half length of whole style, a continuous papillose stigmatic band curved around outside of branch bases then spiralling 1-2 × around each branch. **Capsule** becoming scarious, 12-18 × 17-52 mm, main body ellipsoid, 8-14 × 5-9 mm; wings 3, triangular, ± equal to 1 longer, 8-37 mm, upper margin straight, ± horizontal to ascending up to 45°, lower margin ± straight to elliptically curved, 16-50 mm, tip rounded or acute, 2-8 mm wide distally, wings exceeding capsule 2-5 mm distally, 1.5-4 mm proximally; dehiscence at margins of capsule body.

Chromosome Number: 2n = 22 (White *et al.*, 1946; Legro & Doorenbos, 1969).

Vernacular Name: Santali Name: Dhiri japah *teste Rev. A. Campbell* 8709 (E).

Distribution: Pakistan; North West India, Rajasthan, Himachal Pradesh, Uttar Pradesh, 1000-2000 m; Nepal, 900-2500 m; North-East India, Sikkim and Darjeeling, 150-900 m; North India, Chota Nagpur 380-1300 m; (South India, Madras - almost certainly an error due to a misprinted label; Gamble also collected in N.W. India). See fig. 4.3.

Ecology & Biology: *B. picta* is often found growing on damp, shady, earth banks and terraces, along road sides or in forests (e.g. *Shorea* forest) and woodlands. It is also found growing in and among wet, mossy boulders, and on rock terraces and steep grass slopes and is even found frequently on wet brick walls in some localities.

This species is known as being weedy and will grow in forest shade or almost full sunlight, giving rise to much variation. The leaves may be green, or variegated in many different colour combinations, and the young leaves often display white spots. The flowers may be pink with red or white hairs, or white with red hairs.

DISCUSSION: With a distribution from Pakistan through N.W. India and Nepal to N.E. India, Sikkim and Darjeeling and in the Northern Indian regions of Chota Nagpur and Rajasthan, *B. picta* is one of the more widespread species of *Begonia*. The occurence of the species on Mt. Abu in Rajasthan is interesting. This mountain is famous for its high number of endemic species and has an interesting geological history, containing very old rocks from the Gondwanan continental breakup (R. Mill, pers. comm.). This ancient history may be particularly pertinent for *B. picta* as the species is putatively basal amongst a clade of Asian *Begonia* (see chapter 2, chaaracter 13). The possession of stellate trichomes on the fruit capsule would suggest a basal position for this species (a character shared with a clade of fleshy fruited African *Begonia*, including section *Meziered*). Another point of interest is the similarity of the habit and inflorescence of *B. picta* to some species in section *Platycentrum*, e.g. *B. cathayana*; this would support the hypothesis that section *Platycentrum* is derived from section *Diploclinium* (in the sense used here) [as section *Begonia* in Jin & Wang, 1994].

ADDITIONAL SPECIMENS EXAMINED: INDIA, **RAJASTHAN:** Mount Abu, on way to sun-set point, rainfall 70 inches, 3880 ft, 29.ix.1964, *Rani Ahuja* s.n. (L); **HIMACHAL PRADESH:** Bashahr, Jakleek, 5000 ft, Oct. 1891, *J. H. Lace* 18B, (E [2]); Chamba State, Khajiar to Chamba, 4-6000 ft, 16.vii.1896, *J. H. Lace* 1762 (E); **UTTAR PRADESH:** Mussoorie, Power Pipeline, 4000 ft, Aug. 1914, *Capt. A. Anderson s.n.* (E); Mussoorie, Head work P.P. line, 4500 ft, Aug. 1916, *Capt. A. Anderson s.n.* (E); Mussoorie, 6000 ft, Sept. 1916, *Capt. A. Anderson s.n.*, (E); Mussoorie, 1500 m, 9.viii.1967, *U. C. Bhattacharyya* 37277 (L); Dehra-Dun, Sahasradhara, 6500 ft, 3.ix.1968, *U. C. Bhattacharyya* 37746 (L); Garhwal, 1864, *Falconer* 485 (K); Lachiwala, 16 km SE of Dehra Dun, 400 m, 7.ix.1964, *R. A. Maas Geesteranus* 14098 (L); Voyage de *V. Jacquemont* aux Indes Orient 2394 *pro parte* (P); Voyage de *V. Jacquemont* aux Indes Orient, Kumaon Inferieur, *D. Royle* s.n. (P); near Mussourie, 1869, *G. King* s.n. (E); "*Begonia picta* 21.7" herb. *J. F. Royle* (LIV); "*Begonia picta* 3685 - Mussoorie - wings of capsules unequal, equal in Don" herb. *J. F. Royle* (LIV); "140/2 *Begonia dioica* Don

Prod. p. 225 LSO *echinata* Mussoorea July" herb. *J. F. Royle* (LIV); "*Begonia dioica* Don Prod p. 225 LSO *echinata* Mussoorea July" herb. *J. F. Royle* (LIV); Kumaon, below Naini Tal, 4000 ft, *Strachey & Winterbottom* 2 (P); Himal. Bor. Occ., temp., 4-6000 ft, *T. Thomson* s.n. (P); Simla, 7000 ft, 8.viii.1887, *G. Watt* s.n. (E); Simla, 7000 ft, Aug 1887, *G. Watt* s.n. (E); Simla, 3.viii.1887, *G. Watt*'s handwriting (E); The Glen, Simla, 6000 ft, 3.viii.1887, *G. Watt* s.n. (E); Below the cemetry, Simla, *G. Watt*'s handwriting s.n. (E); "Simla Plants", "collected from same spot; last year's fruit, G. Watt 3.viii.1887", *G. Watt* s.n. (E); **NEPAL:** Chandragari Pass, 7000 ft, 20.vii.35, *F. M. Bailey's collectors,* s.n. (BM); Sonagarhi, 6000 ft, 21.vii.36, *Major Bailey* s.n. (E); Hawidbaugh?, 3.viii.1851, *Dr. Jamieson* 547 (E); Bagmati Zone, Lalitpur District, Codavari temple, 10 miles SE of Kathmandu, 1500 m, 4.ix.1966, *D. H. Nicolson* 2265 (BM); Barikot, 6000 ft, 17.viii.1952, *Polunin, Sykes & Williams* 469 (BM, E); Marma Khola, 3500 ft, 24.viii.1952, *Polunin, Sykes & Williams* 570 (E); Phulchangi, Thuli Beri R., 7500 ft, 10.ix.1952, *Polunin, Sykes & Williams 3303* (E); Marma Khola, 3000 ft, 18.x.1952, *Polunin, Sykes & Williams* 5858 (E); Kali Valley, 3000 ft, July 1886, J. R. Reid (E); North of Taplejung, Tamur Valley, Thapabu Khola, 6000 ft, 2.viii.1956, *J. D. A. Stainton* 1184 (BM, E); Trisuli, 4000 ft, 1.ix.1975, *J. D. A. Stainton* 7453 (E); near Bongakhani, 6000 ft, 22.viii.1954, *Stainton, Sykes, Williams* 3961 (E); near Pokhara, Madi Khola, 3500 ft, 19.vii.1954, *Stainton, Sykes & Williams* 6442 (E); Pokhara, 4000 ft, 6.viii.1954, *Stainton, Sykes & Williams* 6729 (BM, E); Kali Gandaki, Ghasa (S. of Tukucha), 7000 ft, 29.viii.1954, *Stainton, Sykes & Williams* 7534 (E); Butwal, 500 ft, 7.x.1954, *Stainton, Sykes & Williams* 8834 (BM); "Pukka" Chaulisho (near Bajang), 6000 ft, 23.vii.1953, *J.B. Tyson* 110 (BM); "Wall. List No. 3685", "*Wallich,* 3685 a & d" (BM); Kumaon, E.I.C. *Wall.* Cat. 3685, *pro parte* (E); "herb. Ind. Napaul - N. Wallich 1832" (P); "Napalia, N. Wallich Herb. Ind. No. 3685A" (P [2]); Pach Pokri, 1927, *Sir. Clive Wigram* 83 (E); Hitaura, Rapti Valley, 27° 25' N, 85° 05' E, 1800 ft, 22.viii.67, *Williams & Stainton* 8155 (BM); **INDIA, DARJEELING:** Birick, 2000 ft, 10.x.12, *G. H. Cave* s.n. (E); Trista, 1000 ft, 1.ix.19, *G. H. Cave* s.n. (E); Mongpu, 4000 ft, 24.ix.12, *G. H. Cave* s.n. (E); Punkabaree, 3000 ft, 12.ix.1869, *C. B. Clarke* 9031A

(K); ibidem *C. B. Clarke* 9031D (BM); ibidem *C. B. Clarke* 9031H (E); ibidem *C. B. Clarke* 9031L (BM); Teesta, 500 ft, 12.ix.1869, *C. B. Clarke* 9290 (BM); *J. M. Cowan* s.n. (E); **SIKKIM:** ex herb. hort. bot. Calcuttensis, 1857, *T. Thomson* s.n. (L); **BIHAR:** Chota Nagpur, Sirguja State, sent with orchids and flowered in nursery, August 190?, *Rev. L. J. Cardon* s.n. (P); Parasnath, 4200 ft, 3.x.1873, *C. B. Clarke* ?20229 (BM); Parasnath, 4200 ft, 30.ix.1873, *C. B. Clarke* ?21298 (K); Parasnath, 2000 ft, 30.ix.1873, *C. B. Clarke* ?21309B (E); Parasnath, Hazaribagh, 4200 ft, 8.x.1883, *C. B. Clarke* 33727A (BM); Surguja State, Gurguri, 20.x.1947, *W. N. Koelz* 19373 (L); Singhbhum Dist., Porahat, on moist shady bank along Ranchi road below Hessadih, 21.ix.1936, *H. F. Mooney* 154 (K); Chutia Nagpur, Tundi Hills, Pohluria, 1250 ft, 12.viii.1886, *Rev. A. Campbell*, herb *G. Watt* 8709 (E); **?STATE:** Griffith 2598, (P); [**MADRAS:** Garijam District, Valiki, Dec. 1883, *J. S. Gamble* 21734 (K);].

4.5.11 *B. SATRAPIS* C.B.CLARKE IN J.D. HOOKER

PLACE OF PUBLICATION: Fl. Brit. Ind. 2: 638, 1879

TYPE: India, Darjeeling, Rungait, 2000 ft, 29.viii.1869, *C. B. Clarke* 8909A (lectotype designated here: K!); ibidem 20(?30).viii.1869, *C. B. Clarke* 8908B (syntypes: K [2]!); ibidem 23.viii.1875, *C. B. Clarke* 27102D (syntype: BM!); ibidem 23.viii.1875, *C. B. Clarke* 27102F (syntype: E!); ibidem 23.viii.1875, *C. B. Clarke* 27102J (syntype: K!); Sikkim, herb. EIC 2581, *Griffith* s.n. (syntype: K!); Darjeeling, Rungait, 2000 ft, 20(?30).viii.1874, *Dr. Treutler* 623 (syntypes: K [2]!);

OTHER PLACES OF PUBLICATION: Clarke (1881), Linn. Soc. J. Bot. 18: 118; Smith *et al.* (1986), Smithsonian Contr. Bot. 60: 229, Fig. 11.15; Grierson in A.J.C. Grierson & D.G. Long (eds.) (1991), Fl. Bhutan 2(1): 242.

DESCRIPTION: **Acaulescent** to shortly caulescent, tuberous herb, up to c. 50 cm. **Bulbils** not observed. **Stems** erect, up to 4 mm diam.; internodes up to 15(-24) cm, villous, hairs up to 3.5 mm; **stipules** deciduous, triangular-ovate, 2-3 × 1.5-2.4 mm, apex acute, margin ± entire, sparsely pilose. **Petioles** 1-11.5(-18) cm, hirsute, increasing towards apex, hairs up to 1.2 mm; **leaf blade** upper surface covered in short (c. 0.1 mm) glandular hairs, interspersed by longer (0.4-0.8 mm) hairs, lower surface veins hirsute, ± symmetrical, broadly ovate to reniform, 5.2-14.8 × 7.4-19.7 cm, leaf base unequally cordate, lobes 2.9-8.7 cm deep, rarely overlapping, apex rounded (to acute), margin repand, denticulate-ciliate, hairs 0.6-0.8 mm, and c. 0.2 mm, venation palmate-pinnate of 5-7 main veins, 4-5 veins reaching margin in each lobe. **Inflorescence** a terminal dichotomous cyme, up to 10 cm, peduncle 6.6-20.5 cm, hirsute, 9-25 flowered, bisexual, male flowers maturing first; **bracts** tardily deciduous, not differentiated, ovate, 3.2-10 × 1.5-3.2 mm, apex acute, margin denticulate-ciliate, hirsute. **Male flowers: pedicels** 12-20 mm; **tepals** 4, pink; outer pair (sepals) 7-13 × 4.5-9 mm, oblong-(ob)ovate, apex rounded to truncate, margin serrulate-fimbriate outer surface with short (0.1-0.6 mm)

glandular hairs; inner pair (petals) linear-lanceolate to obovate-oblanceolate, 5.6-10.6 × 3-6 mm, apex rounded to truncate, margin entire, glabrous; **androecium** very broadly obovoid; stamens 28-36(-50), filaments ± free, (1.0-)1.6-2.0(-2.4) mm; anthers oblanceolate-obovate (to elliptic), 1-1.2(1.4) mm, connective extended into an oblong tip, dehiscence through slits down entire length of pollen sacs. **Female flowers: pedicels** 11-25 mm, elongating in fruit; **tepals** 5(-6), pink, 4 subequal, obovate to broadly obovate, 5.8-10 × 4-7 mm, apex rounded, margin entire (to serrulate), outer surface with short (0.1-0.2 mm) hairs; 5th (+ 6th) tepal obovate to linear-lanceolate, 5 × 1 mm, apex rounded, margin serrulate; **ovary** obovoid, 4-7.5 × 2.6-5.6 mm, 3 wings, triangular, ± equal in size, upper margins straight, 3-locular, placentae axile, bilamellate, bearing numerous minute ovules on both sides, tomentose; **styles** 3, persistent, fused at base for 0.4-0.8 mm, whole style c. 3 mm, lunate to 2-branched when mature, branches 1.4 - 1.6 mm, a continuous papillose stigmatic band, curving around base of branches then spirally once around top of branches. **Capsule** not observed.

DISTRIBUTION: India, Darjeeling, Rungit, 240-600 m. See fig. 4.3.

ADDITIONAL SPECIMENS EXAMINED: INDIA: UNKNOWN: Darooa Garat, 3000 ft, 3.i.38, *K. Biswas* s.n. (GH, MO).

4.5.12 *B. WILSONII* GAGNEP.

PLACE OF PUBLICATION: Bull. Mus. Paris 25: 281, 1919.

TYPE: Western China, Sichuan, Mt. Omi, Jul 1904, *E. H. Wilson* 4913 (holotype: P not located; holotype (photo): P! isotypes: BM! K!).

DESCRIPTION: Acaulescent - very shortly caulescent tuberous herb up to 50 cm tall. **Bulbils** not observed. **Stem** erect, up to 7 mm diam.; internodes up to 7 cm; **stipules** deciduous, triangular-lanceolate, 2-5 × 1-1.6 mm, apex acute, margin entire. **Petiole** 4-38 cm, ± glabrous; **leaf blade** upper leaf surface very sparsely scabrid to ± glabrous, ± symmetrical, upright, subrotund to ovate, 5-19 × 3-21 cm, leaf base ± equally cordate, lobes 1-4.5 cm deep, spreading apart, apex acuminate to acute, margin shallowly lobed, with acuminate apices, denticulate-serrulate, venation palmate-pinnate of 5-7 main veins, c. 5 veins reaching margin in larger half, 4 in smaller half. **Inflorescence** a terminal, slightly asymmetric dichasial cyme, 3-16 flowered, bisexual, male flowers usually maturing first; **bracts** deciduous, glabrous, barely differentiated, linear obovate at first branching point, c. 6-8 × 1.4 mm, apex rounded, margin entire, lanceolate at later branching points, 3.4-4.8 (-8) × 0.8-1.2(-2.2) mm, apex acute, margin entire. **Male flowers: pedicels** 11 - 16 mm; **tepals** 4, pink; outer pair (sepals) oblong (ob)ovate, 8-11 × 4.5-9.4 mm, apex acute to rounded, margin entire; inner pair (petals) linear-obovate to lanceolate, 6-8.6 × 2-3.8 mm, apex rounded, margin entire; **androecium** obconical, slightly asymmetrical; stamens 10-16, filaments free (to fused up to 0.4 mm), 1.0-1.8 mm, anthers obovoid to ellipsoid, 1.0-1.4 × 0.5-1.0 mm, connective not extended, slits down entire length of pollen sacs. **Female flowers: pedicels** 10-25 mm, elongating in fruit; **tepals** 3, pink, outer pair ovate to oblong-ovate, 9-11 × 6-7.5 mm, apex rounded, margin entire; inner tepal linear lanceolate, 6.6-9 × 2 mm, apex rounded, margin entire; **ovary** fusiform, 10-13 × 2-3 mm, wingless or with 3 narrow ribs, 3-locular, placentae axile, bilamellate in at least part of 2 locules, bearing numerous minute ovules on both sides; **styles** 3, persistent, ± free, whole style 2-3 mm, reniform, becoming lunate when

mature, branches 0.4-0.8 mm, a continuous papillose band encircling top of styles. **Capsule** becoming scarious, 9-12 × 3-3.5 mm, wings not present; dehiscence not observed.

DISTRIBUTION: China, South West Sichuan on Emei Shan at c.1220 m altitude. See fig. 4.3.

ECOLOGY & BIOLOGY: By road side and amongst moist rock.

ADDITIONAL SPECIMENS EXAMINED: CHINA: SICHUAN: Omei Hsien, Mount Omei, Oct. 1941, *C. L. Chow* 4736 (US); Mount Omei, 4000 ft, *Rev. E. Faber* 490 (K); Mt. Omi, Oct. 1903, *E. H. Wilson* 3659 (K); Mt. Omi, Aug 1904, *E. H. Wilson* 4911 (BM, K).

CHAPTER 5 CONCLUSIONS AND FUTURE RESEARCH

5.1 CONCLUSIONS

The conclusions are given here in reply to the original aims of the thesis, as laid out in chapter one.

(a) To produce revised species descriptions for a selection of Asian species currently included in section *Knesebeckia*.

Eleven Asian species are described here and admitted to section *Diploclinium* (Lindley) A.DC., the type of which is *Begonia grandis*. No new species are described. The nomenclature of *B. grandis* is revised after investigation of Irmscher's (1939) infraspecific classification. *B. grandis* subsp. *sinensis* is found to be synonymous with *B. grandis* subsp. *grandis* and consequently *B. martini*, *B. bulbosa* and *B. sinensis* var. *haematoneura* are also synonymised with *B. grandis*. *B. grandis* var. *simsii* is also synonymised with *B. grandis* and a statement made that if the taxon did warrant distinction it would be better recognised as a cultivar. The three varieties of *B. josephi* are found to be synonymous as the variation is continuous and not restricted geographically. The distribution of *B. modestiflora* is found to be much more widespread than previously believed, as the Chinese *B. yunnanensis* and the Indian *B. lushaiensis* are synonymous. A lot of undetermined specimens from Burma and Thailand are identified as *B. modestiflora*, the considerable variation of which is found to be continuous. The Laos material of *B. yunnanensis* var. *thorelii* is also found to be synonymous with *B. modestiflora*. The new combination is made to maintain the varietal status of *B. modestiflora* var. *sootepensis*.

Although desirable it was decided not to produce new descriptions for sections *Knesebeckia*, *Quadriperigonia* and *Diploclinium* as this would be inadvisable for polyphyletic taxa; further data is required.

(b) To test the monophyly of *Begonia* section *Knesebeckia* when containing species from Asia and America.

Using both morphological and molecular evidence, *Knesebeckia* is shown to be polyphyletic. There are several likely different lineages represented in American *Knesebeckia* and at least one independent lineage in Asia.

(c) To determine which species and groups of species should be included in any future studies to delimit the Asian and American species in *Knesebeckia*. And (d) To determine American *Knesebeckia* species relationships based upon morphological data.

Within the American *Knesebeckia* the different lineages appear to be quite disparate. *B. olbia* and *B. dichroa* appear in a clade which is sister to African fleshy fruited species. *B. maynensis* and *B. wollnyi* appear (by extrapolation) to be most closely related to the type of section *Begonia*. *B. incarnata*, the type of *Knesebeckia*, appears in a clade which is sister to the clade including section *Gireoudia*. *B. gracilis* is part of a clade containing species from section *Quadriperigonia* which is the possible sister group to section *Knesebeckia*. Although not all these sections have been included in these analyses, it is suggested that representatives of *Dissepbegonia*, *Hexaptera*, *Huszia*, *Weilbachia* as well as *Begonia* should be considered in any future circumscription of section *Knesebeckia* and in the study of its evolution.

Within Asia, an old mistake in the nomenclature of section *Diploclinium* was located and *B. grandis* was identified as the corrected type of this section. As the Asian and American *Knesebeckia* were found to be polyphyletic, all the Asian species are placed in section *Diploclinium*. The section *Diploclinium* is also polyphyletic but a considerable amount of work is required to define monophyletic units within the section. Together with the Asian *Knesebeckia*, section *Trilobaria*, many of the Thai species already in *Diploclinium* and probably some species in section *Reichenheimia*

will need to be studied in order to delimit this group from other species in *Diploclinium* and those sections associated with *Parvibegonia*.

(c) To produce a preliminary estimate of the phylogeny of *Begonia* based on both morphological and molecular data and to test the congruence of these phylogenies with a view to combining the data sets for a "total evidence" view of the phylogeny of *Begonia*.

The phylogenies estimated from morphological and molecular data for 30 taxa were significantly incongruent. This incongruence was measured by (i) comparison of the branching patterns and bootstrap support of the two cladograms; (ii) calculation of the Mickevich and Farris (Mickevich & Farris, 1981), and Miyamoto (Kluge, 1989) incongruence indices; and (iii) testing the probability that a given data set represents a random partition of the combined data using the partition homogeneity command in PAUP*. It was argued that, in this particular study, the phylogeny produced by the molecular data set is more reliable than the phylogeny based on the morphology data set and that combining the data sets for a "total evidence" view is not conducive to the production of a reliable and conservative estimate of the phylogeny of *Begonia*. Instead it is admitted that the morphological data set is likely to be misleading and that many of the characters may be subject to misclassification resulting in false homologies. With further study it is hoped that a more reliable estimate of phylogenetic relationships can be found with morphological data and that this will result in greater validity for combining the data with a molecular data set to produce a "total evidence" phylogeny.

With regard to the actual phylogeny of *Begonia*, several conclusions could be made. The fleshy fruited species with parietal placentation from Africa are confirmed as the most primitive in *Begonia*. These include sections *Mezierea*, *Squamibegonia*, *Baccabegonia* and *Tetraphila*. There appear to be at least two independent lineages of *Begonia* in America, one represented by species distributed mainly in eastern South America and the other by species in the Andes and Central America. The sister group of

this latter lineage is shown to be species from South and East Africa contained in the sections *Augustia*, *Rostrobegonia* and possibly *Sexalaria* and *Peltaugustia* (these taxa were not sampled here). Again in Asia there seem to be at least two major independent lineages, one represented by *B. grandis* and distributed in more temperate, subtropical and seasonal environments and the other, represented by *B. masoniana* and distributed in more southerly and tropical areas. This suggests two separate radiations in Asia and may also indicate that there have been more than one origin of the genus in Asia. One possible hypothesis to explain this is that one lineage entered Asia via the Middle East and migrated through the Himalayas while the other lineage entered Asia via the rafting of the Indian subcontinent from Gondwanaland to Laurasia. A final point regarding the phylogeny of the genus is that *Symbegonia* is the sister group of section *Petermannia* and its generic status could be questioned.

(f) To investigate the characteristics and evolution of noncoding cpDNA.

The *trn*C - *trn*D chloroplast intergenic region is approximately 3 Kb in length in *Begonia*. This length may vary by up to 1 Kb. The region was found to be AT rich as a result of 9% of the region being composed of simple sequence repeats (SSRs). Sequence divergences within *Begonia* range from 1-9%, while between *Begonia* and *Datisca*, they range from 16-24%. It is noted that these estimates of sequence divergence do not take insertion/deletion (indel) events into account and that these can occur at approximately the same rate as nucleotide substitutions.

Little is known about the evolution of noncoding regions in chloroplast DNA and text books in molecular evolution (e.g. Li, 1997) are limited to discussion of 5' and 3' untranslated regions and pseudogenes. It can be seen in the data presented here and the references cited in chapter 3, paragraph 3.4.3, that the rate of evolution in different noncoding regions varies considerably due to both their selective constraint and the molecular clock operating in a particular taxon. While Golenberg *et al* (1993) cast doubt on the phylogenetic utility of indels in noncoding DNA, I have shown that the indels in

the *trn*C - *trn*D region appear phylogenetically useful and do not exhibit large amounts of homoplasy. The alignment of sequences from *Begonia* species and *Datisca* was slightly problematic but this was not simply due to indels obliterating sequence similarity (as suggested by Zurawski & Clegg, 1987) but was also due to the divergence of the sequences as judged by the nucleotide substitutions.

5.2 FUTURE RESEARCH

Future research intimated by this current study can arbitrarily be broken down into three areas; (1) taxonomic and biosystematic research; (2) morphological research; and (3) molecular research.

5.2.1 TAXONOMIC AND BIOSYSTEMATIC RESEARCH

The taxonomic research undertaken in this thesis has uncovered an enormous amount of work still to be done. Within the American taxa the section *Knesebeckia* is not well defined and requires delimitation from sections *Begonia* and *Quadriperigonia* in particular. Two groups of species have been identified as requiring detailed biosystematic studies to aid in their circumscription; these are the *B. gracilis* group (see chapter 2, paragraph 2.4.3) and the *B. oaxacana* group (see chapter 2, character 65 in paragraph 2.2.2). All the Asian taxa previously in *Knesebeckia* are now placed in section *Diploclinium* but this section is polyphyletic and urgently requires revision. I have included details of all the types for Asian species previously included in *Knesebeckia*. I have also tried to suggest which groups of species will need to be investigated in such a revision (see paragraph 5.1(c), although it may be useful to wait for the outcome of molecular studies involving greater sampling. One problem encountered during this study was the lack of availability of type material for the new Chinese taxa (see preface) and it is imperative to bear this in mind before embarking on such a revision.

From the species revised in this thesis, *B. picta*, *B. modestiflora* and *B. grandis* stand out as taxa suitable for more intensive (biosystematic study). *B. grandis* has an enormous distribution throughout much of China but this is likely to be a result of its use as a cultivated plant. The subspecies *sinensis* was placed in synonymy with *B. grandis* partly because it is likely to be the wild progenitor of the cultivated *B. grandis*, and the type of the species *B. grandis* was cultivated material from Japan (outwith the natural distribution of the species). With the use of molecular markers and population level studies it may be possible to investigate this hypothesis further. It will also be interesting to see if the greater morphological variation present in *B. grandis* subsp. *grandis* compared with *B. grandis* susbp. *holostyla* is mirrored by the amount of genetic variation present in the two subspecies and to confirm that these two subspecies are discrete entities.

B. picta and *B. modestiflora* both have interesting distributions. As explained in chapter 4, paragraph 4.5.10 and chapter 3, paragraph 3.4.2, *B. picta* is widely distributed from Pakistan through N.W. India and Nepal to N.E. India, Sikkim and Darjeeling and in the Northern Indian regions of Chota Nagpur and Rajasthan. Several of the populations of this species are quite disjunt. The morphological variation present in the species varies continuously however, and does not warrant the recognition of any infraspecific ranks. *B. modestiflora* also has a very large distribution from southern North East India (the Lushai Hills) through central Burma, the south west corner of Yunnan, China, Northern Thailand and South West Laos (see chapter 4, paragraph 4.5.8). Again this species displays a large amount of variation but the variation is continous (except for the variety *sootepensis* in Northern Thailand). It would be interesting to study these two species from a phylogeographic viewpoint, to see how their molecular variation is partitioned and test the hypotheses that (a) *B. picta* has migrated through the Himalayas and into Northern India from the West and the hypothetical ancestor of the species therefore entered Asia from the Middle East; and (b) *B. modestiflora*'s nearest relative (e.g *B. minicarpa*) is in Nepal and the species has migrated from there across its current range.

5.2.2 MORPHOLOGICAL RESEARCH

I have suggested that some of the assessments of homology made in chapter 2 might be false and the result of misclassification. The groups of characters which require most investigation are those associated with growth habit and inflorescence structure. The utilisation of anatomical and developmental studies could aid in the assessment of such homologies. I have suggested in chapter 2, paragraph 2.2.2.7 some characters which could prove useful if investigated further. Another avenue of research which has not been investigated fully is cytology and with the provision of a review of the cytology of *Begonia* (Forrest, in prep) this may be better utilised in systematic studies.

5.5.3 MOLECULAR RESEARCH

There are four fronts from which the molecular work I have set out here can be taken further.

(i) The entire region *trn*C - *trn*D should be sequenced for a few selected taxa, e.g. *Datisca*, *B. meyeri-johannis*, *B. grandis* and *B. dregei*. This will increase the reliability of the alignment.

(ii) The sampling of taxa should be increased to provide a robust chloroplast phylogeny for *Begonia*. At the moment sections from America are scantily represented and those sections not included here should be sampled. Notable exclusions from the sampling of African taxa include sections *Loasibegonia*, *Scutobegonia* and *Peltaugustia*, while unsampled Asian taxa include section *Parvibegonia*. From the Asian *Knesebeckia* (= *Diploclinium*) *B. picta* and *B. modestiflora* should be sampled, as the morphological data (see chapter 2) suggests they may be basal within their particular lineages and thus could act as placeholders in a molecular study.

(iii) It will be important to map the precise positions of Tebbitt's (1997) restriction sites (see chapter 3, paragraph 3.4.4) once the entire region *trn*C - *trn*D is sequenced. The reasons for the incongruence of Tebbitt's (1997) RFLP results and my sequence data can

then be ascertained. This research will be both timely and important as authors are now beginning to recommend the utility of the *trn*C - *trn*D region for RFLP studies, e.g. Mes *et al.* (1997).

(iv) Another possibility once the entire region *trn*C - *trn*D is sequenced is the identification and quantification of the indels in the data set. This will allow a useful comparison to be made to Golenberg *et al.*'s (1993) study.

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APPENDIX A: SPECIMENS AND SOURCES OF MATERIAL EXAMINED DURING THE MORPHOLOGICAL STUDIES

B. ACERIFOLIA H.B.K

ECUADOR: prov. Loja, Nudo de Cajanuma, 7 km south of Loja, 8000-8400 ft, 9.vii.1944, *W.H. Camp* E-121 (F): prov. Loja, Loma Larga, Hcda. La Hamaca, Cantón Catacocha, 15.iv.1944, *M. Costa S.* 7850 (F); Bolívar, road Balsapampa - San Miguel, La Guardia, 2500 m, 16-17.v.1968, *G. Harling, G. Storm & B. Ström* 9571 (F); *Sodiro* 594 (F); prov. Azuay, west of Patul, 3 kms between Hualhualcay and Río Patul below Pasas de Pinglión - from near tree-level (in hollow) to rich wooded steep slopes facing northwest, 2670-3275 m, 19.v.1943, *J.A. Steyermark* 52609 (F [2]); prov. El Oro, along Quebrada de Pampa de Los Cedros, tributary to Río Palma, northeast of San Pablo, 2285 m, 12.viii.1943, *J.A. Steyermark* 53801 (F).

PERU: Depto. Cajamarca, Prov. Chota, Ditrito La Paccha, Rejopampa, 2600 m, 21.vii.1993, *J. Cabanillas S.* 756 (F); Dpto. Piura, Prov. Huancabamba, Distrito Canchaque - "Chorro Blanco", 1500-1900 m, 18.iv.1987, *C. Diaz S. y S. Baldeón* 2457 (F; MO); Cajamarca, Santa Cruz, Catache, Upper Río Zaña valley, ca. 5 km above Monte Seco on path to Chorro Blanco, 1500-2000 m, 116-18.iii.1986, *M.O. Dillon et al.* 4390 (F); Cajamarca, Santa Cruz, Catache, Upper Río Zaña valley, ca. 5 km above Monte Seco, near basecamp clearing, ca. 1800 m, 2-4.v.1987, *M.O. Dillon et al.* 4891 (F); Piura - Porculla, Cerro Porculla 3 km to 11 km w. of Continental Divide down W slope of Cerro, 12.vi.1966, *G. Edwin & J. Schunke V.* 3763 (F); Dpto. Cajamarca, Cutervo, Gruta Blanca, Parque Nacional San Andres, 2400 m, 24.ii.1985, *S. Llatas Q.* 1170 (F); Dpto. Cajamarca, Prov. Contumazá, Bosque Cachil, 2500 m, 16.vi.1994, *A. Sagástegui A. et al.* 15307 (F); Dpto. Cajamarca, Provincia San Miguel, Bosque de Quellahorco, al Nor Este de la localidad de Tongod, 2700 m, 14.ix.1991, I. *Sanchez V.*

& A. Briones 5800 (F): Dpto. Cajamarca, Santa Cruz, ca. 3 km (por aire) ENE Monteseco, 1800 m, 9.v.1987, *J. Santisteban C. & J. Guevara B.* 34 (F).

***B. ACUTIFOLIA* JACQ.**

CUBA: shaded bank, along trail, Loma Ventana, above San Blas, Trinidad Mountains, 4.viii.1936, *L.B. Smith et al.* 3309 (K).

JAMAICA: St. Andrews Parish, Blue Mountains, above Cinchona, roadside, shady bank, 1500 m, 14.xii.1958, *J.G. Hawkes et al.* 2254 (K); St. Andrew Parish, steep embankments along road above Hardware Gap, out of Kingston, 600-700 m, 12.i.1979, *W. Scott Hoover* 137 (K).

***B. ADENOPODA* LEM.**

BURMA: Moulmein, 1846, *Lobb* 382 (K [2]); Moulmein, 1859, *Parish* 130 (K); Moulmein, 1861, *Parish* 5 (K).

***B. ALICIDA* C.B.CLARKE**

BANGLADESH: Jadir Pahar, Teknaf, Cox's bazup, rainforest, 28.viii.1984.

BURMA: Moulmein, 1859, Mr. Parish 132 (K).

***B. ANGUSTILOBA* A.DC.**

MEXICO: NAYARIT: km 870, 22 miles southeast of Tepic; steep stony hills in reddish gravelly clay; oak forests with scattered pines, alt. 1150 m., 26.viii.57, *R. McVaugh 16419* (G); **JALISO:** Guadalajara, vii-x.1886, *E. Palmer 282* (K, G); cool banks, 7.x.1889 *C.G. Pringle 2473* (K, B); banks of ravines near Guadalajara, 5000 ft., 8.viii.02, *C.G. Pringle 9806* (K, B); banks of ravines near Guadalajara, 5000 ft., 6.x.1903. *C.G. Pringle* 11451 (B, C, K);

***B. ANNULATA* K.KOCH**

INDIA: Assam, Lushai Hills, Lobawk, Tingtal, and Sibutaleng, 2000-3000 ft, Salem, 5000 ft, vii.1926, *A.D. Parry* 41 (K [3]).

***B. BALMISIANA* BALMIS**

MEXICO: NUEVO LEON: Mexico, Monterez, Allón 4/11 (B); **MEXICO:** Temascaltepec, Rincon, 1960 m, 24.vii.1932, *G.B. Hinton* 1114, (G, K); Temascaltepec, Comunidad, 21.vii.1935, *G.B. Hinton* 7964 (B, K); Temascaltepec, Tejupilco - San-Jose, 17.vii.1935, *G.B. Hinton et al.* 8058 (K); Temascaltepec, Rincon del Carmen, 1460 m, *G.B. Hinton* 17179 (K); **MORELOS:** Cuernavaca, Sierra de Morelos, pine forest, 2000 m, 12.vii.1969, *G.B. Hinton* 1008, (K); **HIDALGO:** Mexico, *herb. Boiss.* 21-8 (G-BOIS [2]); Lava fields above Cuernavaca, 7000 ft., 10.vii.1898, *C.G. Pringle* 6900 (B; BM; G-BOIS [2]; K); **MICHOACAN:** Morelia, Loma Sta. Maria, alt. 2000 m., 29.ii.09, *Arsene* ?43 (?G); red sandy hillside five miles north of Patzcuaro, 13.viii.47, *F.A. Barkley, C.M. Rowell Jr., & G.L. Webster* 2697 (BM); 1800-2000 m., 1.viii.06, *R. Endlich* 1347 (B); Jorillo, to the east above Mata de Patano, *H. Gadow* s.n. (K); pres Morelia a 6800 ft. viii.1840, *H. Galeotti* 202 (G; K); road from Morelia to Mexico City at km 285 from Mexico City, Puerto Vicente Cortes Herrera, shady damp place, rich soil under oaks, alt. 2200 m., 26.ix.58, *J.G. Hawkes, J.P. Hjerting, R.N. Lester* 1574 (C); Coalcoman, S. Torricillas, alt. 1400 m., oak forest, 24.vii.1939, *G.B. Hinton et al.* 13983 (K); Coalcoman, Barroloso, alt. 1400 m., 8.viii.39, *G.B. Hinton* 15074 (B, K); steep rocky slope in open oak woods, cuesta de Aratzipo, km 372 on highway between Quiroga and Zacapu, 21.vii.1948, *H.E. Moore, Jr. & C.E. Wood, Jr.* 21 4042 (BM); roadside ca. 11 miles east of Morelia. Fairly heavy oak woods; heavy red clay soil, alt. 5000 ft. ca., 17.viii.57, *R.M. Straw & D.P. Gregory* 1191 (B); **COLIMA:** ix.1879, *Kerber* 196 (B); 5000-6000 ft., 15.viii.1880, *Kerber* 199 (B); *Kerber* 200 (B); 7000-8000 ft., 15.viii.1880 *Kerber* s.n. (B); **JALISCO:** Sierra del Tigre, 3 miles south of Mazamitla, alt. 2100-2200 m; steep hillsides in pine forest areas, in heavy red clay loam, abundant in one moist hollow, 19.ix.1952, *R. McVaugh* 13071 (BM); **OAXACA:** 1842, *M. Ghiesbreght* ? #1 (K);

UNKNOWN MEXICO:"Ex Mexico in mea fenestra venit Ruiz" (B); **CULT:** ix.1855, Hort Berol. "*Begonia monoptera Link et Otto*" (B).

***B. BISERRATA* LINDL.**

MEXICO:NAYARIT: Nayar, 17 km al NW de Jesus Maria, camino Jesus Maria-La, mesa del Nayar, 22° 15' N, 104° 35' W, elev. 1200 m, 1.viii.1990, *G. Flores F. & R. Ramirez 2159* (NY); **MEXICO:** Temascaltepec, Rincon, alt. 1960 m., 14.ix.1932, *G.B. Hinton* 1672 (G); Temascaltepec, Comunidad, alt. 2700 m., 13.x.1933, *G.B. Hinton 4896* (K [2], G [2]); Temascaltepec, Ipericones, 22.vii.1935, *G.B. Hinton et al. 8081* (K); **JALISCO:** near Guadalajara, 29.vii.1893, *C.G. Pringle 4474* (BM, K & G - 2 sheets); **OAXACA:** Chinantla, 3000 ft., 184?, *H. Galeotti* 205 (G); **CHIAPAS:** Motozintla de Mendoza; south west side of Cerro Mozotal, 11 km north west of the junction of the road to Montozintla along the road to El Porvenir and Siltepec, elev. 2100 m., 27.vi.1972, *D.E. Breedlove 25913* (NY); UNKNOWN: In monte San Felipe, Iunis exeunte, iv.1834, *Andrieux 118* (K [2]); Mexico, 1833, *Andrieux* 247 (G); Sierra San Pedro Nolasco, Talea, &c., Coll. 1843-4, *C. Jurgensen 532* (K, G); *Pavon* s.n. (G-BOIS [2]).

GUATEMALA: Santa Rosa, Jumaytepeque, 6000 ft, Aug. 1892/3, *Heyde & Lux* 3966 (G [2]; K); Vol de Fuego, 5300 ft, Aug 1873, *O. Salvin* s.n. (K); Breñeis, 1400 m. Aug 1921, *Tonduz* 782 (C).

HONDURAS: Octopeque, common on moist bank in forest El Moral on Cordillera Merendon, alt. 1600 m., 27.viii.1968, *A. Molina R. 22302* (BM; G).

CULTA: Chelsea, 15.8.1849, *T. Moore* s.n. (K); Hort. Kew for Bot. Mag. t 4746 *s.l.* s.n. (K).

***B. BOISSIERI* A.DC.**

MEXICO: GUERRERO: Juniper and oak wooded slopes above and east of Taxco on trail to Chacualco, alt. 5800-6200 ft., 18.viii.1948, *H.E. Moore, Jr. & C.E. Wood, Jr.* 4615

(BM); "*Begonia suffruticosus*" *Pavon* s.n. (G-BOIS); in loose granitic cliff 3 miles north of Taxco, 21.viii.1947, *J.B. Paxson, B.L. Westlund & F.A. Barkley* 17M881 (BM).

***B. BREVIRIMOSA* IRMSCH.**

cultivated material, see table 2.1, chapter 2

***B. BULBILLIFERA* LINK & OTTO (=B. GRACILIS VAR. BULBILLIFERA (LINK & OTTO) A.DC.)**

MEXICO: GUANAJUATO: 5 km al ENE de Comanjilla, camino a Arperos, mpio de Guanajuato, 2080 m, *R. & J.D. Galván* 3163 (NY); La Escalera, mpio. de Atarjea, 1150 m, 18.ix.1990, *E. Ventura y E. López* 8755 (F); **MEXICO:** 1.5 mi. from Temascaltepec along hwy, back toward Toluca, 17.viii.1972, *Dziekanowski et al.* 1999 (NY); Temascaltepec, Vigas, 1080 m, 28.viii.1932, *G.B. Hinton* 1493 (BM; NY); Temascaltepec, Rincón, 1960 m, 9.ix.1932, *G.B. Hinton et al.* 1543 (K); Temascalatepec, Chorrera, 1.viii.1935, *G.B. Hinton et al.* 8132 (NY); **MICHOACAN:** environs de Morelia, Sungnato, 2100 m, 9.viii.1909, *G. Arsène* 2877 (B; BM; NY); Coalcoman, Barroloso, 1270 m, 7.viii.1939, *G.B. Hinton et al.* 15068 (NY); **COLIMA:** Colima, ix.1879, *Kerber* 195 (B); **JALISCO:** moist banks near Guadalajara, viii.1893, *C.G. Pringle* 4504 (B; E); **UNKNOWN:** *Bates* s.n. (K [2]); *Ehrenberg* 32 (B); *Schiede* s.n. (B); **CULT.:** Hort. Berol., 8.x.1880, *O. Hoffmann* s.n. (B); Hort. Berol., ix.1829, *Schiede* s.n. (B); Hort. Carbr., ix.1836, *sine coll.*, s.n. (B).

***B. CONVOLVULACEA* (KLOTZSCH) A.DC.**

BRAZIL: *Huber* 204 (K Photo); *Sello* 636 (K); Serra de Maranguape, Estado de Ceura, x.1919, *E. Ule* 9074 (K Photo); "1825", *Herb. Saup. Vien* (K).

***B. CORDIFOLIA* (WIGHT) THWAITES**

CEYLON: near Vellavaya, 3.i.1928, *A.H. Gaston* 1645 (K); Arawakumbura, bet. Lunugala & Bibile, Badulla District, 450 m, 15.xii.1972, *Jayasuriya & Tiruvengadum*

1006 (K [2]); Kotatalawa, between Mahiyangana & Uraniya, Badulla District, 160 m, 15.xii.1972, *Jayasuriya & Tiruvengadum* 1007 (K); Hasalaka, Kandy District, 80° 56' E, 7° 21' N, 100 m, 15.xii.1972, *Jayasuriya & Tiruvengadum* 1008 (K); Ududaha (mile 39), Bintenna Pass, Kandy District, 150 m, 19.i.1974, *Jaysuriya et al.* 1420 (K); *Thwaites* 3584 (K); 1857, *Herb. Wight* s.n. (K).

INDIA: Malabar, vi.1836, *Herb. Wight* 1030 (K).

***B. CRENATA* DRYAND.**

INDIA: South Concan, Canara & Mysore, *Law* s.n. (K); Canara & Mysore, Dhar war & Bellamy Districts, *Law* s.n. (K); Sany Khand, river bank, 1600 ft, x.1919, *L.J. Sedgwick* 6983 (K); Concan, herb. Ind. Or. Hook.f. & Thomson, *Stocks* s.n. (K [6]); North & South Concan, Mt. Lous, *sine coll.* s.n. (K).

***B. CUERNAVACENSIS* ZIESENH.**

MEXICO: MORELOS: forests near toll road from Mexico City to Cuernavaca on path east from hairpin bend, ca. 2300 m, 5.x.1958, *J.G. Hawkes et al.* 1618 (C); Sierra Morelos, Cuernavaca, 1900 m, 25.x.1969, *G.B. Hinton et al.* 17421 (K); **PUEBLA:** S. Nicolas de los Ranchos Santiago Xalitzintla, 19° 05 N, 98° 28' W, bosque de pino-encino, alterada, suelo negro, arenoso, 2530 m, 15.ii.88, *P. Tenorio L.* 15123 (F; K).

***B. DEALBATA* LIEBM. (=B. GRACILIS VAR. DEPAUPERATA)**

MEXICO: CHIHUAHUA: 43.5 km al N de Basigochi, Carr. A Creel, 14.ix.1983, *R. Torres C.* 3657 *y P. Tenorio L.* (F); **MEXICO:** Valle de Bravo, Rancho San Lorenzo, near the town of Valle de Bravo, 14.i.1943, *C.L. Gilly Sr.* 26 (NY); Valle de Bravo, Zitacuaro - Nihuatlan, 2550 m, 4.x.1938, **author** (NY); Temascaltepec, Volcán, 5.xi.1932, *G.B. Hinton et al.* 2506 (K; NY); Temascaltepec, Las Mesas, 21.x.1934, *G.B. Hinton et al.* 6785 (B; NY); Temascaltepec, Cumbre de Tejupilco, 22.xi.1934, *G.B. Hinton* 7020 (C); **MICHOACAN:** Zitacuaro, Zitacuaro - San Andrez, 14.x.1938, *G.B.*

Hinton et al. 13358 (K); **GUERRERO:** Mina, Armenia, 2260 m, 23.x.1936, *G.B. Hinton* 9758 (K); Mina, Pilas, 1560 m, 28.ix.1937, *G.B. Hinton et al.* 10739 (C; NY [2]); Mina, Aguazarca-Filo, 2.xi.1937, *G.B. Hinton et al.* 11257 (F); Mpio. Atlixtac, 24 km al E. de Chilapa por la carretera a Tlapa, 2070 m, 29.x.1979, *S.D. Koch et al.* 79162 (NY); Mina, Sierra Madre del Sur, Petlacala, 1850 m, 15.xii.1937, *Y. Mexia* 8966 (B); open ridges and slopes with sparce cover of low second growth oaks on granitic soil at summit of mountains between Chilpancingo and Tixtla, 6000 ft, 5.x.1949, *H.E. Moore Jr.* 5243 (BM); Texquitxin, Chalapa, x.1929, *L. Schultze Jena* 109 (B); **OAXACA:** Sn Jeronimo C., Miahuatlan, 33.2 km al SW de Sn J. Coatlan, brecha a Piedra Larga, 1550 m, 16° 12' N, 96° 57' W, 8.viii.1990, *A. Campos V.* 3306 (F); Cordillera, 1840, *Galeotti* 192 (K); Sierra de Oaxaca, *Liebmann* 164 (C); *Liebmann* s.n. (B).

***B. DICHROA* SPRAGUE**

cultivated material, see table 2.1, chapter 2

CULT: Jardin Botanique de Montréal, *Raymond & Gougeon* 2829-50 (B);

***B. DIPETALA* GRAHAM**

INDIA: Kakamalai, Thiashola, Nilgiris, vi.1933, 1988, *E. Barnes* 199 (K); Courtallum, Tamil Nadu, 800 m, 5.vi.1976, *C.E. Ridsdale* 17 (K); environs Devicolam, Kerala, Sholas Devicolam-Periyar Road mostly beyond the gap, Cardamon Hills, 24.iii.1980, *C.E.Ridsdale* s.n. (K).

CEYLON: Sellaka-oya Sanctuary, N. of Baduluwela, Monaragala Distr. 80° 25' E, 7°05' N, low altitude, 5.v.1975, *A.H.M. Jayasuriya* 2065 (K).

***B. DREGEI* OTTO & A.DIETR.**

cultivated material, see table 3.1, chapter 3

SOUTH AFRICA, Natal, Cape Port St Johns, coastal forest in cult., Mar-71, *Admiraae* 2286 (K); Port St. John, Pondoland, Cape, 11.ii.1919, *C.E. Moss* 4621 (K).

***B. FALCILOBA* LIEBM.**

OAXACA: rocks and damp places at 3000 ft. Cordillera. iv-xi.1840. *H. Galeotti* 193 (K); Intertrapiche de la Concepcinis Fortonleper, *Liebmann* 165 (C [4]); ibidem, x.1842, *Liebmann* s.n. (B); Loc. 19 km al NW de Piedra Larga carr. Puerto Escondido. Hierba de 30 cm con flores blancas. Veg. Bosque mesófilo alterado, 1.viii.84. *R. Torres C.* 5813 *y C. Martinez* (F); **UNKNOWN:** Sierra San Pedro Nolasco, Talea, &c. Coll. 1843-4. *C. Jurgensen* 807 (K).

CULT: Hort. Bot. Berol. 13.xii.1978, *Schwerdtfeger* 6279 (B).

***B. FERNALDIANA* L.B.SM. & B.G.SCHUB.**

MEXICO: **GUERRERO:** Mina, Manchon, bank by the river, 1200 m, 27.viii.36, *G.B. Hinton et al.* 9343 (K); *ibidem*, alt. 1200 m, in oak woods, 2.ix.36, *G.B. Hinton et al.* 9425 (NY); Serre du Crest, *Micheli* 1899 (G [2]); *s.loc.*, *Micheli* 1901 (G).

***B. FLOCCIFERA* BEDD.**

INDIA: on rocks near Kodamadi, Tinnevelly Hills, i.1933, *E. Barnes* 201 (K); Madras, Seugaeferi, Tinnevelly Hills, ix.1914, *J.S. Gamble* 191 (K).

CEYON: Peradeniya Gardens, in glasshouse, *J.E. Senaratna* 2, 3.vii.1928 (K).

UNKNOWN: sine loc., xii.1871, *Beddome* 217 (K).

***B. GEMMIPARA* HOOK.F. & THOMSON**

INDIA: Darjeeling, 7800 ft, 7.viii.1875, *C.B. Clarke* 26875 (K);Darjeeling, 9000 ft, 3.ix.1875, *C.B. Clarke* 27380C (K); *ibidem*, *C.B. Clarke* 27380E (K); Darjeeling, Tanglo, 10000 ft, ix.1880, *J.S. Gamble* 8464 (K); Sikkim, *Griffith* 2566 (K); Sikkim,

temp Regio, 7-10000, 29.viii.1874, *J.D. Hooker* s.n. (K [3]); Sikkim, 9000 ft, 12.ix.1874, *Treutler* 751 (K).

NE NEPAL: ridge between Kabeli Khola and Omje Khola NE of Yamphudin, 27° 28' N, 87° 55' E, 2370 m, 23.ix.1989, *KEKE* 901 (K).

***B. GOEGOENSIS* N.E.BR.**

cultivated material, see table 3.1, chapter 3

***B. GRACILIS* H.B.K. (=*B. GRACILIS* VAR. *MARTIANA* (LINK & OTTO) A.DC.)**

MEXICO: CHIHUAHUA: Sierra Canelo, Rio Mayo, 30.viii.1936, *H.S. Gentry* 2517 (K); Canon de St. Diego, 17.ix.1891, *C.V. Hartman* 774 (BM; F; NY); 4 km al SW de Quirare, camino a Batopilas, 1870 m, 17.ix.1983, *R. Torres C.* 3730, *P. Tenorio L.* (F; NY); Sierra Madres near Colonia Garcia, 7000 ft, 29.viii.1899, *C.H.T. Townsend & C.M. Barber* 287 (B; BM; E; NY [2]); **NUEVO LEON:** and just east of border into Tamaulipas, Dulces Nombres, on moist shady banks above dry stream course in canyon on east side Cerro Linadero, 24° N, 99.5° - 100.5° W, 1900 m, 11.viii.1948, *F.G. Meyer & D.J. Rogers* 2938 (E); Zaragoza, Cerro del Viejo, 15 mi. w. Dulces Nombres, 2400 m, 20.viii.1948, *F.G. Meyer & D.J. Rogers* 3055 (E); **SAN LUIS POTOSI:** 28.ix-3.x.1903, *E. Palmer* 202 (NY); 22° N, 6000-8000 ft, 1878, *C.C. Parry & E. Palmer* 263 (BM; NY); **SINALOA:** Ocurahui, Sierra Surotato, 6000-7000 ft, 27-30.viii.1941, *H.S. Gentry* 6161 (NY); Ocurahui, Sierra Surotato, 6000-7000 ft, 1-10.ix.1941, *H.S. Gentry* 6260 (NY); **GUANAJUATO:** San Miguel de las Casitas, mpio. de Xichú, 2300 m, 8.ix.1990, *E. Ventura y E. López* 8675 (F); **HIDALGO:** San Vicente, 7900 ft, 16.viii.1937, *G.L. Fisher* s.n. (NY); about 2 kms above Apulco on road to Agua Blanca, 7200 ft, 7.ix.1948, *H.E. Moore Jr. & C.E. Wood Jr.* 4891 (BM); **MEXICO:** Vallée de Mexico, Pédregél, 2.viii.1865, *E. Bourgeau* 649 (B; K; NY); Mount Popocatepetl, 8250 ft, 21.vii.1935, *G.L. Fisher* 35449 (NY); Temascaltepec, Tequesquipan, 2480 m, 19.viii.1932, *G.B. Hinton et al.* 1341 (K); Temascaltepec, Bejucoa, 610 m, 6.x.1932,

G.B. Hinton et al. 2005 (BM; NY); Temascaltepec, Temascaltepec, 1750 m, 11.x.1932, *G.B. Hinton et al.* 2054 (K [2]); Texcoco, San Miguel Tlaixpan, 2400 m, 23.ix.1984, *A.Ventura A.* 4287 (BM; NY); Temascaltepec, Ypericones, 19.xi.1934, *G.B. Hinton et al.* 7000 (K; NY); Temascaltepec, Comunidad, 13.viii.1935, *G.B. Hinton et al.* 7988 (B; NY); Tepotzotlan, Presa de la Concepción, 2400 m, 23.xi.1979, *A.C. Luque* 6 (NY); Peohegal, viii.1927, *E. Lyonnet* 165 (BM); rocky hills, Lecheria, 7500 ft, 23.viii.1904, *C.G. Pringle* 11993 (B; f); Valley of Mexico, near Tlalpam, 20.viii.1903, *J.N. Rose & J.H. Painter* 6462 (NY); Coyonanan, 2.x.1904, *E. Seler* 4135 (B); Tezcolzingo, Vallée de Mexico, 25.ix.1910, *E. Seler* 5373 (B); Nicolas Romero, Cahuacan, 2700 m, 26.ix.1982, *A. Ventura A.* 41311 (F); Nicolas Romero, San Jose del Vidrio, Cahuacan, 2600 m, 12.ix.1982, *E. Ventura V.* 31 (F; NY); **MORELOS:** Coajomulco, mpio. de Huitzilac, 2500 m, 27.ix.1970, *J.M.Díaz Moreno* 156 (NY); Sierra de Tepoxlan, 21.ix.1903, *J.N. Rose & J.H. Painter* 7238 (NY); **VERACRUZ:** Las Vigas to Jalapa, Perote, 6700 ft, 17.ix.1938, *E.K Balls* B5459 (BM; K); Orizaba, 1853, *F. Müller* 2205 (NY); Tlacolulan, 1600 m, 16.viii.1973, *E. Ventura A.* 8861 (NY); **MICHOACAN:** Coalcoman, Barroloso, 2400 m, 21.x.1939, *G.B. Hinton et al.* 15360 (B; NY); Uruapan, Tancitaro, 1950 m, 26.x.1940, *G.B. Hinton et al.* 15583 (K); **COLIMA:** San Colima, 6000 ft, 15.viii.1880, Kerber 197 (B); **JALISCO:** Northeastern slopes of the Nevado de Colima, below Canoa de Leoncito, steep cut-over mountainsides in fir zone at head of Barranca de la Rosa, 2800 m, 10.x.1952, *R. McVaugh* 13414 (BM); **OAXACA:** Dto. De Coixtlahuaca, km 9 del camino de Ruta 190 a Coixtlahuaca, 2360 m, 8.viii.1985, *D.H. Lawrence* 4788 *& A. Garcia M.* (F); **UNKNOWN:** Monterey, Rio de fundición, 8.ii.1912, *Abbón* s.n. (B); *Aschenborn* 190 (B); T. *Bernhardi s.n. (B);* ex herb. Collegii SS. Trin., Dublin, *Coulter* 1416 (K; NY); illeg. *C. Ehrenberg* 32/s.n. (B [5]); 1830, *Graham* 315 (K); in Brasilia collegit P. Claussen, 1846, *E.R.F. Hohenacker* s.n. (B); Amecameca, 8600 ft, viii.1904, *O. Kuntze* 23643 (NY [3]); *Liebmann* s.n. (B); Specim. Sine loci indicat. Ex pl. *Martii* 1845 (NY); Xochimulco, 3.x.1910, *C.R. Orcutt* 4262 (BM); Salto de Agua, x.1905, *C.A. Purpus* 1791 (NY); Anganguio, *Scheide* s.n. (B [2]); viii.1835, *Schmitz* s.n. (B [2]); 20.ix.1884, *W. Schumann* 1201 (B). **CULT:** Hort. Berol., 8.x.1880,

O. Hoffmann s.n. (B); sine loc., *K. Koch* s.n. (B); Jardin Botanique de Montréal, viii.1958, 1004-57; Hort. Berlin, 31.x.1856, *Paul* s.n. (B); Hort. Berol., ix.1838, *sine coll.* s.n. (B); Hort. Berol., 1844, *sine coll.* s.n. (B).

***B. HERACLEIFOLIA* SCHLTDL. & CHAM.**

MEXICO: VERA CRUZ: Meirador, ii.1839, *J. Linden* 34 (K); **MICHOACAN & GUERRERO:** Rives du Rio Texpan, 29.i.1899, *E. Langlassé* 820 (K); **GUERRERO:** Vallecitos, Montes de Oca, 27.i.1938, *G.B. Hinton* 11762 (K); **OAXACA:** Distr. Choapam, Yaveo, trail west to Rio yaveo, shady bank in forest, 435 m, 18.3.1938, *Y. Mexia* 9174 (K); **CHIAPAS:** Ocosingo, Chajul sobre el río Lacantún, 150 m, *E. Martínez S. y R. Lombera* 26186, 26.i.1992 (K); **UNKNOWN:** Valle de Cordora, 24.xii.1865-66, *M. Bourgeau* 1583 (K [2]); Huasteca, near Tantoyucam Wartenburg, 1859, *L.C. Ervendberg* 334 (K).

GUATEMALA: Guatemala Depto., 5000 ft, ii. 1890, *J.D. Smith* 1859 (K); Santa Rosa, Depart. Santa Rosa, 4000 ft, i.1893, *Heyde & Lux* 4190 (K).

HONDURAS: Pueblo Viejo, 1700 ft, 18.ii.1934, *W.A. Schipp* S-695 (K).

***B. HINTONIANA* L.B.SM. & B.G.SCHUB.**

MEXICO: **MEXICO:** *G.B. Hinton* 2050 (K); Temascaltepec, Ixtapan, 1000 m, 23.x.32, *G.B. Hinton* 2284 (K); Temascaltepec, 21.x.34, *G.B. Hinton et al.* 6786 (K); Temascaltepec, Cumbre de Tejupilco, oak woods, 22.xi.34, *G.B. Hinton et al.* 7021 (K); **GUERRERO:** Mina, Manchon, 28.ix.36, *G.B. Hinton et al.* 9611 (B; K); Montes de Oca, Vallecitos, oak woods, 2.x.37, *G.B. Hinton et al.* 11453 (K).

***B. IGNEA* WARZ. EX A.DC.**

MEXICO: GUERRERO: montes de Oca, Vallecitos, oak woods, 11.vii.37, *G.B. Hinton* 10593 (K); rd. to Acahuizotlan, 1 mi W of jct. Mex hwy 95, 3 mi N of Agua de Obispo,

2900 ft., cut over, partially wooded road bank, 2.vii.82, *W.W. Thomas* 2871 *with J. Rawlins & O. Sholes* (NY).

COSTA RICA: San José, Cantón de Puriscal. Lower slopes of Cerro Bola along Rte 239, just N of San Martín. 9° 44' N 84° 23.5' W, 850 m alt. locally abundant on damp slope at roadside, 21.vii.88, *M. Grayum* 8603, with *B. Hammel, N. Zamora & M.M. Chavarría* (F); *Hoffman* 876 (B [2]); secondary growth along Río Virilla, 4 km N of the center of San José, Prov. heredia-San José, alt. 1100 m, 22.ix.71, *R.W. Lent* 2151 (F); San Francisco de Guadalupe, Oct. 1892, *H. Pittier* 7150 (G); sur les bords d'un ruisseau pres d' Asseri 17.viii.1889, *A. Tonduz* 1299 (B; BM); Bord d'un ruisseau pres de San Juan, 28.9. 1889, *Tonduz* 1299 bis (G); Bord des Ruisseaux a la Verbena pres Alajuelita 1000 m, viii. 1894, *A. Tonduz* 8919 (B; BM; G-BOIS [2]).

CULT.: Hort. *Schoenbrunn*, Schott mis (B); Hort. bot Berol., 19.ix.1854 de *Wars.* Guatemala" (B); hort. Berol. 1851 (?1891) (B); hort. bot. Berol (B; C); Hort. Hamburg, x.1853 (B).

***B. IMPERIALIS* LEM.**

GUATEMALA: Cubilquitz, Depart. Alta Verapaz, 350 m, vi.1900, *H. von Tuerckheim* 7626 (K).

CULT: Hort Kew, Ill. Hort. 1861, t. 274, 23.iii.1877, *E. Brown* s.n. (K); Hort. viii.1882, *Mr. Orpet* (K).

***B. INCARNATA* LINK & OTTO**

MEXICO: EDO. VERACRUZ: s.l. *S. Avendano R. et al.* 13 (K); Yecuatla, El Mirador Carretera Naolinco Misantla, alt. 1200 m, 4.ii.76, *S. Avendano R. et al.* 128 (NY, K); Jalapa,4.xi.1908, *C.R. Barnes & W.J.G. Land 559* (K); Region d'Orizaba a Tzhuatlancilla, 20.v.1866, *E. Bourgeau* 2494 (K); Actopan, El Descabezadero debajo de la Caida de Agua, 19° 31' N 96° 39' W, 28.v.77, *G. Castillo C. & S. Avendano R.* 172

(NY); Acajete, Barranca del Pixquiac, arriba de la Vega., 30.iii.1988, *M. Chazaro B., L. Robles, P. Hernandez de Ch.* 5407 (NY); Jalapa, Tronconal, alt. 1400 m, 10.xii.72, *J. Dorantes, M. Acosta, A. Calles & W. Marquez* 01885 (BM); Sierra San Pedro Nolasco, Talea, & c., 1843-4, *C. Jurgensen 615* (K); Orizaba, Aserradero de Santa Cruz, vii.1853, *F. Muller* 1662 (NY); Jilotepec, Rincon del Muerto 19-37 N, 96-57 W, alt. 1250 m, 25.viii.82, *H. Narave F. & L. Pacheco* 158 (NY); Tlalnehuayocan, 1 km above and NW of San Andrés Tlalnehuayocan, 19° 34' N 96° 58' W, alt. 1700 m, 22.iii.83, *M. Nee, K. Taylor & H. Narave F.* 26181 (NY); Yecuatla, along a very winding road from Naolinco to Misantla, 13 km by road south of turn off to Yecuatla and 6 km by road north Paz de Enriquez, ca. 19° 51' N, 96° 48' 30" W, alt. 1200 m, 2.iv.83, *M. Nee, K. Taylor & H. Narave F.* 26392 (NY); Tonayan, 1 km al SE de Tonayan, alt. 1700 m, 11.xi.75, *R. Ortega O. et al.* 9 (NY); Jalapa. Carr. México-Veracruz, km 457. 500 m por la desviación hacia Plan Cedeño, alt. 1600 m., 29.iii.82, *P. Sanchez P.* 42 (NY); Jalapa, Alt. 4000-4500 ft., xii.1894, *C.L. Smith* 686 sheet 1 & 2 (NY); Cerro de San Cristobal near Orizaba, W 09705 N 1850, Montane mesophilous forest. West facing, semi-shade. Growing in rich loam, humus soil overlaying volcanic substrata, 1400 m, 10.xi.93, *M. Sparrow & P. Brewster* VERA 48 (K); Mun. Coatepec. Briones, 28.v.77, *V. Vazquez T.* 41 (NY).

CULT: 27.xii.1838, *H.B. Basil* s.n. hort. (NY); Mexico, Calipa in mart, Ex Herb Hort. Bot. Hafn. *Liebm.* s.n. (K); *B. incarnata* Link & Otto Ic. Pl. Rar. Berol. p. 37. t. 19 (K); Ex Herb. E (K).

B. JOHNSTONII OLIVER EX HOOK.F.

TANZANIA: Tanganyika, Lushoto District, 24.v.1953, *R.B. Drummond & J.H. Hemsley* 2728, (K); (T3), Tanga Region, Usambara Rainforest Research Project, Lushoto Distr., west Lushoto, rocky, secondary grassland, 1500 m, 12.iii.1984, *W.R. Mziray* 84808/A (CULT UPS) (K); (T6), Morogoro District, Kanga Mountains, 0600 S 3743 E, montane mist forest, 780 m, 5.vii.1983, *R.M. Polhill, J.C. & J.M. Lovett* 4965, (K); Iringa

District, north part of Gologolo Mountains, 7 40' S, 36 53' E, in wet grass near stream, 1500 m, 13.ix.1970, *M. Thulin & B. Mhoro* 957, (K); Kilosa Distr., Ukaguru Mountains, Ihanga rock, 6 26' S, 37 03' E, steep sometimes vertical rock, 1450 m, 2.vi.1978, *M. Thulin & B. Mhoro* 2862 (K);

***B. LOBATA* SCHOTT**

BRAZIL: Minas Geraes, Oure Prete-Estrada para Andrinhas, a 1 km da Esc. de Farmacia de Oure Preto, 1250 m, sele argilese, vermelho, ma beira da estrada, 4.vi.1978, *Fontella* 1078 (K); Minas Geraes, 1841, *Gardner* 5145 (K); Minas Geraes, Serra do Espinhaço, summit and upper slopes on south side, Serra da Piedade, iron-rich soil, ca. 5 km north of Caeté, ca. 2000 m, 20.i.1971, *H.S. Irwin et al.* 28779 (K); Minas Geraes, Serra do Espinhaço, lower slopes of Pico de Itacolomí. cerrado and gallery forest with some campo, ca. 3 km south of Ouro Preto, ca. 1650 m, 31.i.1971, *H.S.Irwin et al.* 29516 (K); Minas Geraes, Serra do Cipó, Fda. Palacio (Mun. Jaboticatuba), 8.viii.1972, *G. Hatschbach* 30073 (K); road from Hotel Chapeu do Sol, kms 120-140, summit of Serra de Cipó, 1200-1300 m, 8.viii.1960, *B. Maguire et al.* 49086 (K); "Ewaldia Ferruginia Kl." *Sello* s.n. (K); "Herb. Surfio Vien" 1821 *sine coll.*, s.n. (K); "Minas Geraus Garden" viii.1840, *sine coll.* 5745 (K); Minas Geraes, 1845, *Widgren s.n.* (K).

***B. LUDWIGII* IRMSCH.**

ECUADOR: Prov. Chimbor., Hcdaa. "La Carmela", estrivaciones inferiores Cord. Occ., Sibambe, 1000-1600 m, 16.viii.1943, *M. Acosta Solis* 5328 (F); Prov. Chimborazo, Cañon of the Río Chanchan, about 5 km north of Huigra, 5000-6500 ft, 19-28.v.1945, *W.H. Camp* E-3317 (F; G [2]); Tal des R. Chanchen bei Naranjapata, 530 m, 25.ix.1933, *L. Diels* 1204 (B); Prov. Azuay, Hacienda Yubay, at Sanagüín, on south side of Río Patul, 850 m, 26.v.1943, *J.A. Steyermark* 52699 (F [2]); Prov. Azuay, rich rainforest jungle, steep slopes aloing Río Patul between Hacienda Yubay and Hacienda San José de Caimotán, in region of Sanagüín, 850 m, 28.v.1943, *J.A. Steyermark* 52716

(F [2]); Prov. El Oro, trail between Portovelo and Zaruma, 640-1155 m, 22.viii.1943, *J.A. Steyermark* 53985 (F).

***B. MALACHOSTICTA* SANDS**

cultivated material, see table 3.1, chapter 3

***B. MANNII* HOOK.F.**

CAMEROON: Efulen, on old log over river, 7.x.1895, *G.D. Bates* 404 (K).

EQUATORIAL GUINEA: Bioco: Luba Riaba, cerca de Rilaja, 32NMJ6078, malezas junto a la carretera, 720 m, 29.vi.1986, *F. Casas* 10068 (K [2]).

NIGERIA: Benin Province, Benin, Okomu Forest Reserve, Rare on sandy bed of dried up stream in R. Nikrowa R.H., O.F.R.; also on a tree trunk leaning across stream; not seen elsewhere, 10.xii.1947, *J.P.M. Brenan* 8469 (K); Uyo District, Eket, along the road to James Town, 4.x.1964, *B.O. Daramola* FHI 55280 (K); Ogoja Province, Ikom District, Aboabam, about 1/4 mile from village on Boje path, secondary forest near stream, 9.xii.1950, *R.W.J. Keay* FHI 28178 (K); Calabar Province, Oban Group Forest Reserve, near Aningeje on Calabar - Mamfe R. road, lowland rain forest, margin of forest, 13.i.1959, *R.W.J. Keay* FHI 37731 (K); Benin, Sapoba, Usomgbe Forest Reserve, In partially depleted high forest (T.S.S. area), scrambling over fallen log, 31.i.1948, *P.W. Richards* 3900 (K).

***B. MARTABANICA* A.DC.**

BURMA: Tenasserim and Andamans, Moulmein, 1837, *Helfer* s.n. (K); Moulmein, 1846, *Lobb* 393 (K [2]).

INDIA: *Lobb* 175 (K);

***B. MASONIANA* IRMSCH.**

cultivated material, see table 3.1, chapter 3

CULT: Jardin Botanique de Montréal, 6.vii.1971, no. de culture 2341-54 (B [2]).

***B. MAYNENSIS* A.DC.**

PERU: Río Cenepa, vicinity of Huampami, ca. 5 km E of Chávez Valdívia, ca. 78° 30' W, 4° 30' S, 200-250 m, 3 km arriba de la boca de la Huampami, 25.vii.1978, *E. Ancuash* 1101 (F); trail E of Huampami to Shaim, 600-1750 ft, 1.viii.1974, *B. Berlin* 1902 (B); Lugar Huampami, Quebrada Pantamentsa, 810 ft, 6.vi.1973, *R. Kayap* 893 (F); Quebrada Wampushik entsa, 940 ft, 13.vi.1973, *R. Kayap* 963 (F); Camino de jutui entsa, 700-800 ft, 30.vii.1974, *R. Kayap* 1385 (F); Loreto, Balsapuerto (lower Rio Huallaga basin), 350-550 m, 29.viii.1929, *E.P. Killip & A.C. Smith* 28476 (F); Dpto. Loreto, Soledad, on Río Itaya, ca. 110 m, 20-22.ix.1929, *E.P. Killip & A.C. Smith* 29553 (B; F); Dpto. Loreto, Mishuyacu, near Iquitos, 100 m, ii-iii.1930, *G. Klug* 1065 (F); Dpto. San Martin, Zepelacio, near Moyobamba, 1100 m, vii.1934, *G. Klug* 3716 (F); Dpto. Loreto, Above Pongo de Manseriche, mouth of Rio Santiago, 21.xi.1931, *Y. Mexia* 6130 (F; G); Dpto. Loreto, Above Pongo de Manseriche, hills to left of Río Marañon, 250 m, 26.xii.1931, *Y. Mexia* 6348 (F; G [2]); San Martin, Dtto. Tarapoto, Carretera de Tarapoto - Yurimaguas, km 12 -16, 2250 ft, 23.viii.1978, *M. Rimachi Y.* 3829 (F); prope Tarapoto, 1855-6, *R. Spruce* 4859 (E; G); Stromgebiet des Maranon von Jquitos aufwärts bis zur Santiago - Mündung am Pongo de Manseriche, ca. 77° 30 W, 1924, *G. Tessmann* 4002 (B); Stromgebiet des Maranon von Jquitos aufwärts bis zur Santiago - Mündung am Pongo de Manseriche, ca. 77° 30 W, 1924, *G. Tessmann* 4180 (B); Loreto, an Felsen des Pongo de Chilcayo, Tarapoto, x.1902, *E. Ule* 6467 (B; G).

ECUADOR: Napo, Río Aguarico, Dureno (30 km east of Santa Cecilia), 14.iii.1968, *G. Harling, G. Storm & B. Ström* 7650 (F); Napo, Armenia Vieja at Río Napo, ca. 12 km south west of Coca (Puerto Francisco de Orellana), 12.i.1973, *H. Lugo S.* 2649 (F); Napo, Guamanyacu, road Coca (Puerto Francisco de Orellana) - Lago Agrio, ca. 40 km north east of Coca, 18.11.1973, *H. Lugo S.* 3457 (F); Pastaza, Río Curiacu, ca. 8 km

west of Puerto Sarayacu, 19.x.1974, *H. Lugo S.* 4212 (F); Pastaza, Pacayacu on the Río Bobonaza, c. 116 km NW of Sarayacu, 10.viii.1979, *H. Lugo S.* 5257 (F); Prov. Pastaza, along log road to Canelos, 10 km from highway top Puyo, ca. 500 m, 25.vii.1980, *M. Shemluck* 331 (F).

BRAZIL: Acre, Mpio. Tarauacá, Rio Muru, 12 km above confluence with Rio Tarauaca, 20.ix.1968, *G.T. Prance et al.* 7409 (F).

***B. MEYERI-JOHANNIS* ENGL.**

KENYA: Tusid fishing park, E. Aberdares, 7000 ft, xii.1933, *E.R. Napier* 5895 (K); Tanganyika, 23.10.1956, Mrs.. *H.M. Richards* 6739, (K); (K4), Nr. Castle Forest Station, Kirinyaga District, 0022 S 3719 E, female plant hangin in festoons from trees, with terrestrial and aerial roots; on trees at edge of forest, by road, 2070 m, 12.ix.1971, *Mrs. S.A. Robertson* 1579 (K); East Province, Tanganyika, Uluguru Mts., Morogooro District, Mar-55, *S.R. Semsei* 2049 (K); Central Province, Embu District, southern slopes of Mt. Kenya, montane forest just beyond Kangaiti Tea Factory, ca. 5 miles north of Kerugoya on tarmac road, a forest of Cassipourea, Tabernaemontana, Lasianthus, Piper, Macaranga, Neoboutonia; climbing over trees and shrubs, 10.x.1976, *R.W. Spjut & S. Muchai* 4664 (K); Tanganyika, Kuu Moshi District, Machame Nkuu, Kilimanjaro Forest Reserve, in camphor forest, 7000 ft, xi.1960, *R.C. Steele* 120, (K).

UGANDA: Kigezi, mile 12 road from Kabale to Kanaba Pass, in wood on swamp composed largely of Syziguim, 5000 ft, viii.1952, *E.M. Lind* 112, (K); Kigezi, Kiruruma Swamp, swamp forest of Syzygium cordatum and Myrica kandtiana, 6500 ft, 10.ix.1952, *E.M. Norman* 1799 (K).

RWANDA: Wisumo, Commune de Gisovu, Centre forestier, Kibuye, forêt de montagne, 2300 m, 16.ii.1980, *D. Bridson* 408, (K); route Butare - Cyangugu, env. de Rwasenkoko, Gikongoro, 2000 m, 28.v.1981, *G. Troupin* 16263 (K).

***B. MICHIOACANA* L.B.SM. & B.G.SCHUB.**

MEXICO: MICHOACAN: Distr. Apatzingan, Loc. Aguililla, alt. 800 m, forest barranca, 18.ix.39, *G.B. Hinton et al.* 15186 (NY).

***B. MICROCARPA* A.DC.**

ECUADOR: "in Andibus Ecaudorensibus, 1857-9, *R. Spruce* 5070 (G);

COLOMBIA: Depto. Del Huila, Cordillera Oriental, vertiente occidental, abajo de Gabinete en la hondonada del Abra de San Andrés, bosques, 1900-2100 m, 24.iii.1940, *J. Cuatrecasas* 8606 (F); Depto. Del Valle, Cordillera Occidental, vertiente oriental, Hoya del río Pichindé, entre Quebraada de Juntas y El Recreo, 2070-2260 m, 7.viii.1946, *J. Cuatrecasas* 22006 (F).

***B. NEMORALIS* L.B.SM. & B.G.SCHUB.**

MEXICO: MICHOACAN: Distr. Coalcoman, Loc. Barroloso, alt. 1200 m, woods by Ixtala river, 7.viii.39, *G.B. Hinton et al.* 15063 (B).

***B. NOVO-GRANATAE* A.DC. (=*B. ROSACEA* PUTZ.)**

VENEZUELA: Táchira Edo., Uibante Dtto., ca. 4 km above Pregonero on road to Bailadores, secondary growth and old cultivated areas; very rocky red adobe soil on steep cliffy hillsides, 1400-2550 m, 28.viii.1973, *S.S. Tillett & KW Honing* 738-489a (K).

COLOMBIA: Cundinamaria, Sasuima - M. Baldenaima, i.1876, *E.F. André* 322 (K).

***B. OAXACANA* A.DC.**

MEXICO: VERACRUZ: La Joya, Perote, 6500 ft., 17.ix.1938, *E.K. Balls & W.B. Gourlay B5464* (BM; K [2]); Mpio: Acajete Barranca del Pixquiac, alt. 2000 m, 30.iii.88, *M. Chazaro B., L. Robles H. & P. Hernadez de Ch. 5420* (NY); **JALISCO:** about 15 miles southeast of Autlan; barranca in pine-oak-fir forest above stream-bed, in mountains near trail from Chante to Rancho Manantlan and thence southeasterly 3-4 hours with pack

animals toward El cuarton; alt. 2400-2600 m., 13.iv.49, *R. McVaugh 10266* (BM); **OAXACA:** Cordillera; Woods at 6000 ft., iii.1840, *H. Galeotti 196* (K); **CHIAPAS:** 1864-70 *Ghiesbreght* 683 (K); San Andres Larrainzar: Paraje Naxinich, 1 km de la tierra fria, milpa cabecera Larainzar, 6000 ft, 11.ii.1988, *L. Gonzalez G. 426* (NY); Pueblo nuevo, ii.1840, *Linden 39* (K); Fray Cesca, near Siltepec, alt. 2000 m, 13.iii.45, *E. Matuda 5263* (NY); Mpio Tenejapa: Rancho banabil Alt. 2200 m, 26.iv.1983, *A. Mendez Ton 5920 (A. Shilom Ton)* (NY); San Cristobal de Las Casas: Santa Cruz en San Filipe, 15.xi.1986, *A. Mendez Ton 9641* (Maria Concepcion Mtz. de Lopez) (?); Mun. Pueblo Nvo., Solistahuacan En Reseva Natural Yerbabuena, Frente a la clinica Yerbabuena, 2 km al NW de Pueblo Nuevo Solistahuacan, elev. 1850-2150 m., 15.ii.1990, *A. Reyes G. 1656, with R. Hampshire, P. Stafford, M. Heath & A. Long* (BM); Zinacantan, cerro muk'tarriz Huitepec, 10.iii.1985, *A. Shilom Ton 823* (NY); de Tenejapa; La Cuerva yashanal, 15.iii.1984, *A. Shilom Ton 7401* (NY).

GUATEMALA: San Miguel Uspantan, Dept. Quiche, alt. 6000 ft. iv.1892, *Heyde & Lux 3095* (K); Cerro Chichoy, Sierra Madre Mountains, about 10 km NW of Tecpan, Dept. Chimaltenango, alt. 2200-2300 m, 25.xii.72, *L.O. Williams, A. Molina R. & T.P. Williams 41790* (BM).

HONDURAS: Distrito Central, Rancho Quemado, 4000 ft., 3.iv.1970, *W.T. Gillis 9623* (NY).

EL SALVADOR: Dept. Santa Ana, El Trifinio, Cordillera miramundo, mountain of montecristo, alt. 2000-2200 m, 27-31.i.1966, *A. Mollina R., WC Burger & B. Wallenta 16787* (NY); East slope of Los Esesmiles, 14° 21' N, 89° 09' W, c. 2250 m, 13.iii.42, *J.M. Tucker 1029* (K).

COSTA RICA: Prov. San Jose; along the trail from Canaan to Chirripo via Los Angeles, above (north of) the Rio Talari, 9° 30' N, 83° 32' W, alt. 3000 m, 19-22.i.1970, *W.C. Burger & R.L. Liesner 7498* (BM); Prov. San Jose; Cordillera dee Talamanca, Pacific slope of the Chirripo Massif; elev. 3000-2700 m., 6.iv.1969, *G. Davidse & R.W. Pohl*

1636 (NY); Prov. San Jose; Cordillera de Talamanca, Cerro Chirripo Massif; 2500 m. 6.iv.1969, *G. Davidse & R.W. Pohl 1652* (NY); Limon; Chirripo National Park, by path between Agua Potable and highest point of cloud forest on way to Chirripo, c. 2800 m 17.ii.1983 *N. Garwood, M. Gibby, R.J. Hampshire & C.J. Humphries 1316* (BM); San Gerardo, 5 km NW of crater Irazu, Cartago, 2000 m, ii.1983, *L.D. Gomez 19874* (NY); Prov. San Jose, Providencia road, 2.5 km S of km 76 of Interamerican highway (Rt. 2), Cerro Vueltas, 2800 - 2900 m., 9° 37' N, 83° 49' W, 16.i.87, *S.R. Hill 17885 (with D.S. Barrington & J. Davis)* (NY); Heredia - Cerro Chompipe, N. of San Rafael, 2000 m 29.viii.64, *K. Lems 640829(01)* (NY); *ibidem*, *K. Lems 640829(02)* (NY); Var Blanca de Sarapiqui, north slope of Central Cordillera, between Poas and Barba volcanoes, 1800 m, i.1938, *A.F. Skutch 3414* (K); Provincia de San Jose, Near Finca La Cima above Los Lotes, North of El Copey, 21-22.xii.1925, *P.C. Standley* 42776a (K); Prov. San Jose; about 3 km NW of Casajal near the union of the Casajal and Bajo Maquina Rivers. From along the floodplain of these rivers, elev. 1750 m, 30.vii.1972, *J. & C. Taylor 11250* (NY); Prov. San Jose; about 3 km NW of Casajal near the union of the Casajal and Bajo Maquina Rivers. From the floodplain of these rivers, elev. 1750 m, 30.vii.1972, *J. & C. Taylor 11283* (NY); prov. San Jose, about 3 km NW of Cascajal near the union of the Cascajal and Bajo Maquina rivers. From along the floodpalin of these rivers, elev. 1750 m. 30.vii.1972, *J. & C. Taylor 11328* (NY).

PANAMA: Prov. Chiriqui, Volcan Baru (E. slope) deep draw west of Finca Yen, 8000 ft. 17.iii.79 *B. Hammel, W. D'Arcy & J. Averett 6453* (BM); Prov. Chiriqui; on road to Pasio Respingo E of Cerro Punta, 7000 ft, 2.iv.79, *B. Hammel, W. D'Arcy, E.C. Hill, S. Schwartz O. & H. Wolcott 6626* (BM); Chiriqui; 47.2 km from Pan American Highway at beginning of rough road into Baru National Park; 8° 53' N, 82° 36' W, 2270 m, 20.ii.86, *Scott Hoover 563* (BM).

***B. OLBIA* KERCH.**

BRAZIL: illeg., 1878, *Rohl* s.n. (K); São Paulo, 1829, *Sello* s.n. (B).

CULT: Bot. Gart. Berlin-Dahlem, 31.vii.1963, *Ra* 172 (B); Bot. Gart. Berlin-Dahlem, 25.vii.1983, *Schwerdtfeger* 14873 (B); Bot. Gart. Berlin-Dahlem, 10.ii.1955, *T.H. Slussen* s.n. (B); 20.1.1955, *T.H. Slussen* s.n. (B); hort. Dahlem, 1.vii.1912, *sine coll.* s.n. (B); hort. Dahlem 29.x.1914, *sine coll.* s.n. (B).

cultivated material, see table 3.1, chapter 3

***B. PALMATA* D.DON**

China: **GUANGDONG:** Kwangtung, Sha lo Shan, Lo-Lo-ha village, Sin-fung District, 6-25.vii.1938, *Taam Y.M.* 980 (K); **GUIZHOU:** Houang-tsau-pa, 1918, *J. Cavalerie* 7568 (K); **YUNNAN:** 1917-1919, *G. Forrest* 15650 (K); 1917-1919, *G. Forrest* 17777 (K [2]); Megtze, SE mountains, 5000 ft, *A. Henry* 9204A (K); Megtze, SE mountains, 5000 ft, *A. Henry* 9205 (K); Feng Clên Lin, S. of Red River, 6000 ft, *A. Henry* 10368 (K); Mengtze, SE forest, 5000 ft, *A. Henry* 11420 (K); Szemao, mt. ravines, 4-5000 ft, *A. Henry* 12250A&B (K); *ibidem*, *A. Henry* 12250 (K); Teng-yueh, *E.B. Howell* 119 (K).

***B. PEDATA* LIEBM.**

MEXICO: PUEBLA: Boca del Monte, "Moist Rocks", viii.1907, *C.A. Purpus 2696* (B); **GUERRERO:** Texquihzin bei Chilopa, x.1929, *L. Schultze Jena 85* (B); "El Carrizal" 9 km, al W de Iyotla, Carr. a Filo de Caballo, de Chichihualco, Alt. 2000 m, 12.viii.1982, *P. Tenorio L.* 1305, *L. Hernández S. y C. Romero de T.* (?); **OAXACA:** Sierra de San Felipe, 7500 ft, 11.x.1894, *C.G. Pringle* 4955 (B; BM; K); Near San Antonio Eloxochitlán, District of Teotitlán, 12.vii.38, *R.E. Schultes & B. Pablo R. 453* (K); *White 1083* (B); 1859, *Cuming* s.n. (?); Mountains north Pacific, Cordillera, 6-8000 ft., 1840, *H. Galeotti 191* (G).

***B. PELTATA* OTTO & DIETRICH**

MEXICO: VERACRUZ: Coatepec, 1 km. SE of main Jalapa - Huatusco highway, 5 km SW of bridge over Rio Los Pescados, 5 km (by air) SE of Tuzamapan, 19° 21' N, 96° 50' W, 680 m, 19.iii.1983, *M. Nee & K. Taylor 26034* (NY).

GUATEMALA: Inter S. Miguelito et Sto. Thomas. i.1878, *Bernoulli & Cario 2842* (K); Depto. Baja Verapaz; along road (national Hwy. 5) between Guatemala City and Rabinal, between Granados and Rabinal; southern slopes of Sierra de Chuacus, 2.8 mi. N of El Chol; roadside vegetation on steep rocky dry slopes, 15° 00' N, 90° 29' W, 1560 m, 25.i.87, *T. B. Croat & D.P. Hannon 63584* (NY); Depto. Izabal. ca. 6 km SE of mariscos, Lake Izabal, alt. 0-600 m. A.S.L., 15° 15' - 15° 35' N, 89° 0' - 89° 25' W, 26.iv.66, *G.C. Jones, G.R. Proctor, Facey 3132* (NY); Depto. Sacatepequez, dry secondary forest, lower slopes Volcan de Fuego, 3 km south west of Alotenango, alt. 1200 - 1300 m, 15.i.74, *Louis O. & T.P. Williams 43474* (BM); Count *Solms*, Corn. viii.1885; (K); Mirador in Jan. *sine coll.* (K).

***B. POCULIFERA* HOOK.F. VAR. POCULIFERA**

CAMEROON: rocky dry river bed with light forest, 2250 m, 3.ii.1962, *F.J. Breteler et al.* MC 161 (K); Cameroon Mt., *Hutch & Metcalfe* 1, (K); Mont. Golep (ou Ngoro, 1585 m), 336 km au N. de Bafia - feuille ion 1/200 000 linte, en foret submontagnarde, 1550 - 1585 m, 26.xi.1969, *R. Lettouzey* 9584, (K).

NIGERIA: Ogoja, Obudu Cattle Ranch, northern ranges, epiphyte on tree trunk in riverine forest, ca. 5200 ft, 12.iv.1973, *J. Medler* 786, (K).

***B. PORTILLANA* S. WATSON**

MEXICO: SINALOA: Tepic, 1924, *J. Gonzalez Ortega* 404 (K); Tepic, Acaponeta, vii.1897, *J.N. Rose* 1509 (B); **NAYARIT:** Mirador del Aguila, ca. 14 miles north of Tepic, 450-575 m, 10.vii.1957, *R. McVaugh* 15293 (G); **DURANGO:** Toyaltita, Toyaltita,

92 km al SW de San Miguel de Cruses, 1480 m, 24° 09' N, 105° 57' W, 7.vii.1984, *P.Tenorio L.* 6286 *y C. Romero de T. & T.P. Ramamoorthy* (F); **JALISCO:** base of east slope of the barranca SE of Guadalajara, by the powerhouse, about 11 mile downstream from bridge, 1020 m (a few hundred yards up slope of river), 23.vi.1956, *D.P. Gregory & G. Eiten* 164 (NY); Barranca, near Guadalajara, vi.1886, *E. Palmer* 143 (BM; K); moist ledges near Guadalajara, 3500 ft, 10.vii.1895, *C.G. Pringle* 4741 (B; BM; G; K); 4.vi.1897, *J.N. Rose* 1734 (K).

***B. PRISMATOCARPA* HOOK.F.**

Sosef (1994)

***B. PROLIFERA* A.DC.**

BURMA: Moulmein, *Parish* 3 (K); Moulmein, 1862, *Parish* 17 (K); Moulmein, *Parish* 18 (K); Moulmein, 1862, *Parish* s.n. (K).

***B. PUTII* CRAIB**

Thailand, Payap, Doi Chiengdao, 19.x.1926, *Put* 403 (ABD).

***B. QUADRIALATA* WARB. SUBSP. QUADRIALATA**

CAMEROON: Munaiya R., west of Mamfe, in coarse sand of roadside bank, *C.D. Adams* 1338 (K); Kumba District, Korup N.A. Forest Reserve, , high forest, river bank, 23.vi.1951, *J. Olorunfemi* 30646 (K); 4 km SE of Nguélémendouka, along road to Doumé, open vegetation near creek, sandy soil, 700 m alt., 23.xi.1961, *F.J. Breteler* 2125 (K);

NIGERIA: Ondukpani, 14 miles north of Calabar, vertical sandy and shady bank at side of track through forest, 18.xii.1944, *B.L. Burtt* B1 (K); Ogoja Province, Ikom District, Afi River Forest Reserve, near Aboabam, marshy ground by stream under high forest, 9.xii.1950, *R.W.J. Keay* FHI 28188 (K).

***B. RAJAH* RIDL.**

cultivated material, see table 3.1, chapter 3

***B. RHODOCHLAMYS* L.B.SM. & B.G.SCHUB.**

MEXICO: MICHOACAN: Apatzingan, Loc. Rancho Viejo, 650 m, forest, 18.ix.1939, *G.B. Hinton* 15190 (K); **GUERRERO:** Galeana, Loc. Aloyac, 25-100 m, 1.5 m high, 10.viii.1939, *G.B. Hinton* 14529 (K).

***B. ROXBURGHII* A.DC.**

Species description in Tebbitt (1997).

***B. RUBELLA* BUCH.-HAM. EX D.DON**

cultivated material, see table 3.1, chapter 3

Nepal, Gossain Than, *Wallich* 3686 (G).

***B. SALAZIENSIS* (GAUD.) WARB. IN ENGL.**

La Réunion, Ceuillaume, Vallée Rivière St. Denis, sous bois de forêt degradée au dessous de l'Ilet, 500 m, 31.xii.1971, *Th. Cadet* 3390, (K); Réunion, Mare Longue, above St. Philippe, forest, pathside at forest margin, 500 m, 25.ii.1975, *MJE Coode* 4952 *with Th. Cadet* (K); Mascareignes, Bourbon, 1813, *Carmichael* s.n., (K); Mascareignes, Bourbon, *Richard* s.n., (K); Mauritius, s.l., (K).

***B. SANDTII* ZIESENH.**

MEXICO: SINALOA: Concordia, Ternstromemia along small logging road near Lobcras Microwave Station, 1570 m, 4.viii.1980, *D.E. Breedlove* 44993 & *F. Almeda* (MEXU); **JALISCO:** wet mossy ledges near Guadalajara, 25.ix.1889, *C.G. Pringle* 2456 (B; NY [3]); wet ledges of the barranca of Guadalajara, 5000 ft, 19.x.1903, *C.G. Pringle* 11452 (B).

***B. SERICONEURA* LIEBM.**

BELIZE: Yucatan Peninsula, Gracie Rock, Sibun River, 28.iii.1935, *P.H. Gentle* 1537 (K); Yucatan Peninsula, El Cayo District near Camje 6, *P.H. Gentle* 2364 (K); Jacinton Hills, 400 ft, 10.iv.1934, *W.A. Schipp* 1300 (K); caves, 100 ft, 1931, *W.A. Schipp* S-182 (K).

HONDURAS: Honduras, San Pedro Sula, Depart. Santa Bárbara, 1000 ft, ii.1887, *C. Thieme* 5238 (K); Aguan River valley, foothills near the village of Medina, vicinity of Coyoles, Depto. of Yoro, 625 ft, 26.vii.1938, *T.G. Yuncker et al.* 8642 (K); in thicket along trail, slopes of Mt Cangrejal back of Ceiba, on the mountain slopes and coastal plains, vicinity of Lalceiba, Depto. of Atlantida, 16.vii.1938, *T.G. Yuncker* 8469 (K).

NICARAGUA: 1867-8, R. Tate 122 (K).

UNKNOWN: Chontales, *Dr. Seamaun* 46 (K).

***B. SOCOTRANA* HOOK.F.**

SOCOTRA: ii-iii.1880, *Prof. Bayley Balfour* 419 (K [2]); 1897, *Mr. & Mrs. Theodore Bent* s.n. (K); Reiged Plateau, 4 km SW of Hadiboh, 740 m, 21.ii.1989, *A.G. Miller et al.* 8335 (K); Hagghiher Mountains, 12° 35' N, 54° 03' E, Jebel Shihali, 3500 ft, 19.v.1967, *A.R. Smith & J. Lavranos* 748 (K); xii.1891, *sine coll.* s.n. (K).

CULT.: Hort. Kew, 1880, *Dr. Balfour*, Bot. Mag. t. 6555 (K [2]).

***B. SUTHERLANDII* HOOK.F.**

TANZANIA: (T4), Kigoma District, Kasye Forest, 5 41' S, 29 55' E, wet moss and fern covered banks along stream in evergreen forest, 900 m, 19.iii.1994, *S. Bidgood, F. Mbago & K. Vollesen* 2819, (K); (17), Rungwe District, Kiejo Volcano, west face, volcanic lavas and ashes of 1800 AD, in lava block niches, 8.v.1975, *Hepper, Field & B. Mhoro* 5387, (K);

SOUTH AFRICA: Natal, Berguilk District, Oluiiershoek Pass, common in rocky stream gully in forest, 5500 ft, 18.ii.1970, *O.M. Hilliard* 4910, (K); Natal, Transvaal, Pilgrims rest did Hebranberg, mossy boulders above stream, 6000 ft, 19.i.1969, *Hilliard & Burtt* 5995, (K); Transvaal, Zwisihen Barberton u Piggs Peak (Swaziland), 900-1600 m, 6.ii.1959, *E. Werdermann & H.D. Obberdieck* 2176, (K).

***B. TAYABENSIS* MERR.**

cultivated material, see table 3.1, chapter 3

PHILIPPINES: Umiray, Province of Tayabensis, Luzon, v-vi.1917, *M. Ramos & G. Edaño Bureau of Science* no. 29054 (K).

***B. TENERA* DRYAND.**

CEYLON: Kalukola, 28.viii.1927, *A.H. Gaston* 894 (K); Yatibariya, between Giniyathena & Kitulgala, Kandy District, 100m, 26.vi.1972, *Jayasuriya et al.* 845 (K); Kalugala, Kandy District, Central Province, 80° 26' E, 7° N, 160 m, 19.ix.1972, *Jayasuriya* 844 (K [2]); vicinity of 29/16 road marker between Rattota-Midlands, Matale district, 80° 42' E, 7° 30' N, 760 m, moist shady bank, 11.xii.1972, *Jayasuriya* 989 (K); Singampoeslej, Montes Palameos, 8.xi.1795, *Rottler* s.n. (K); vii.1884, *H. Trimen* (K); Ceylon, *Walker* s.n. (K).

CULT.: Sept. 1864, Thwaites 2808 (K); Hort. Kew, 1837, *Thwaites* s.n. (K).

***B. ULMIFOLIA* WILLD.**

VENEZUELA: "found only as the elevation of the Melastomeae but is then very common on the road from La Suayra to Caryacilo" iv.1854, *M.Burchill* s.n. (K); Cerro Bolívar, Estado Bolívar, locally frequent in forest between Pilot Plant and Tunnel E-4, 600-675 m, 28.ii.1953, *J.J. Wurdack* 34447 (K).

***B. UNIFLORA* S.WATSON**

NUEVO LEON: Mpio. Linares, near Ejido Los Alamos, 7.2 mi. south of Mex. 60, 25° 45' N, 100° 44' W, c. 600 m, 28.x.1982, *J. Grimes et al.* 2368 (NY); Silla Mt. Monterrey, 2.x.1937, *L.A. Kenoyer* 230 (F); Los Alamillos, 23.xii.1947, *M.M. Lacás* 526 (F); Hacienda Pablillo, Galeana, 27.viii.1936, *M. Taylor* 235 (F); Cañon el Diente, Sierra Madre Oriental, ± 20 km al sur de Monterrey, mpio. de Monterrey, 25° 34' N, 100° 14' W, 700 m, 21.ix.1989, *J. Vladés R. et al.* 1951 (NY).

***B. URUAPENSIS* SESSÉ & MOÇ.**

MEXICO: NAYARIT: about 4 miles east of Jalcocotán, on road to Tepic, 750 m, 5.x.1952, *R. McVaugh* 13365 (G [2]); at km 20 on the Tepic-Compostela road; 1150 m. growing in wet ravine, 4.x.63. *B.G. Schubert* 2002 & *M. Sousa S.* (NY; XAL); at km 22 on the Tepic - Compostela road, *B.G. Schubert* 2005 & *M. Sousa S.* (XAL); **DURANGO:** alt 4700 ft., 15.viii.1897, *J.N. Rose* 2297 **(?)**; **MEXICO:** Temascaltepec, Loc. Tejupilco, 1340 m, 16.x.32, *G.B. Hinton et al.* 2206 (K; NY [2]); Temascaltepec, Loc. Temascaltepec. Rocky Hill, alt. 1900 m, 18.xi.32, *G.B. Hinton* 2428 (F; K); Temascaltepec. Cliffs by the river. 29.x.34, *G.B. Hinton et al.* 6803 (K [2]; NY); Temascaltepec, Loc. Cumbre de Tejupilco, oak woods. 22.xi.34, *G.B. Hinton et al.* 7022 (K [2]; NY); **MICHOACAN:** 3 km al W de La Cruz de Cachan, Mpio. Aquila, 90 m, 29.ix.1980, *B. Guerrero C.* 1010 (XAL); Coalcoman, 1000 m. 3.xi.38, *G.B. Hinton et al.* 12505 (K [2]); Coalcoman, Huizontla, Forest, 660 m, 15.xi.38, *G.B. Hinton* 12579 (B; F; K); **JALISCO:** La Huerta, Estación de Biologia Chamela, 22.ix.1981, *E.J. Lott* 498 & *J. Arturo Solís M.* (XAL).

***B. WALLICHIANA* LEHM. (=*B. FRANCONIS* LIEBM.)**

MEXICO: Vicinity of Victoria, Temaulipas, 320 m, 1.ii-9.iv.1907, *E. Palmer* 168 (K); San Luis Potosi, Tampasopo Canyon, 13.vi.1890, *C.G. Pringle* 3100 (K).

***B. WEBERLINGII* IRMSCH.**

EL SALVADOR: Chalatenango, San Fransisco del Tunel, *F. Weberling* 1429 (B; K - photo).

***B. WOLLNYI* HERZOG**

BOLIVIA: Dpto. La Paz, Prov. S. Yungas, Basin of Rio Bopi, San Bartolome (near Calisaya), 750-900 m, 1-22.vii.1939, *B.A. Krukoff* 10493 (F); Santa Cruz, Sara, region de campos, Buena Vista, 450 m, 5.ix.1925, *F. Steinbach* 7218a (B; F; G); NW Chigmaca u Iñalmasi, 1200 m, 20.ix.1927, *C. Troll* 460 (B); San Buena Ventura, 1400 ft, 14.xi.1901, *R.S. Williams* 600 (BM).

BRAZIL: Seriugal S. Francisco, Rio Aore, vi.1911, *E. Ule* 9649 (B [2]).

***DATISCA CANNABINA* L.**

INDIA: W. Himalaya, Pangi (Chamba State), Fenn Range Forest, Eler, Hassukli, 8500 ft, 3.viii.1899, *J.F. Duthie* s.n. (K); NW Himalaya, Upper Chenab Valley, 6000 ft, 1879, *B.H. Baden-Powell* 146 (K).

IRAN: Ardabil reg., Khushavar, Caspian Coast, gravel deposit by river, 0-50 m, 16.viii.1966, *P. Crisp* 129, (K [2]); 28.6.1936, *A.C. Troll* 534 (K);

***HILLEBRANDIA SANDWICENSIS* OLIV.**

Bot. Mag. t6953, 25.5.1887, s.l., (K);

HAWAIIAN ARCHEPELAGO: Kauai, Kokee, 1100 m, 31.v.1982, *V. Balgooy* 4244, (K[2]); Molokai, Waikolu gorge, along pipeline trail, near tunnel, 13.vii.1938, *L.M. Cranwell & C. Skottsberg* 2627 (K); Molokai, wet gullied region between Waikulu valley and probably northern base of Puu alii, open wet slope, 10.iv.1928, *O. Degener* 9760 (K); Molokai, Popohia, vi.1912, *C.N. Forbes* 85 (K ex Mo); E Maui, above Ahuida, woods near ?kulele, vii.1910, *C.N. Forbes* 175M (K); Maui, Wailuka Valley, *Hillebrand* 466 (K [2]); Oahu, Molokai, Maui, 1870, *Dr. W. Hillebrand* s.n. (K [2]);

Hanalei, Kauai, XI 1866, *H. Mann & W.T. Brigham* (K); E. Maui, Haleakala Crater, Koolau Gap, Wailau Waterfall, Oct. 1910, *J.F. Rock* 8631 (K); Hawaii, 1885, *Mrs. Sinclair* 1 (K).

***SYMBEGONIA SANGUINEA* WARB.**

cultivated material, see table 3.1, chapter 3

APPENDIX B: PCR RECIPE FOR AMPLIFICATION OF CPDNA REGION *TRN*C-*TRN*D

NH_4	5 µL
Mg^{2+}	2 µL
dNTPs	2.5 µL
*trn*C	1 µL
*trn*D	1 µL
Taq	0.5 µL
DNA	1-10 µL
H_2O	to make up total volume of 50 µL

NH_4	160 mM
Tris-HCl	670 mM
Mg^{2+}	50 mM
dNTPs	16 µl of each in 736 µl H_2O working stock dNTPs - 50mM soln.
Primers	10 µl of working stock (50mM) primer in 190 µl H_2O
EtBr	conc. 10 mg / mL; I used 0.02 µL in 1 mL.

APPENDIX C: PCR PROGRAMME FOR AMPLIFICATION OF *TRN*C-*TRN*D

File 93	94°C - 4 min.	1 cycle	(linked to 92)
File 92	92°C - 45 sec.		
	58°C - 45 sec.	35 cycles	(linked to 91)
	72°C - 2 min.		
File 91	72°C - 10 min.	1 cycle	(linked to 80)
File 80 (Soak File)	4°C ∞		

APPENDIX D: PCR CYCLE SEQUENCING PROTOCOL

Use thin walled PCR tubes.

Terminator Ready Reaction Mix*	8.0 µL
Template: PCR product, 10-30 ng / µL	3-6 µL
Primer	5 pmole (=1 µL) (3.2 pM is recommended)
dH_2O	make up volume
Final volume	20 µL

Overlay reaction mixture with light oil.

PCR Profile:

30 sec @ 96°C

15 sec @ 50°C 25 cycles

4 min @ 60°C

Soak File @ 4°C

* Dye Terminator Cycle Sequencing AmpliTaq FS®

APPENDIX E: PURIFYING CYCLE SEQUENCING PRODUCT

1. For each reaction, prepare a 0.5 mL microcentrifuge tube by adding the following:

2.0 μL 3M Sodium acetate, pH 4.6

50 μL 95% ethanol

(Note 3M sodium acetate, pH 5.2, and 3M potassium acetate, pH 5.6, appear to work equally well.)

2. Transfer the entire 20 μL (better to use about 18.5 μL) contents of the reaction tubes to the microcentrifuge tubes containing the ethanol solution, ensuring the pipette tip is oil free. Vortex and place on ice for 10 min.s.

3. Centrifuge at max speed for c. 20 min.s.

4. Carefully aspirate the ethanol solution with a micropipetter. Remove as completely as possible.

5. Rinse the pellet by adding 250 μL 70% ethanol, leave for 30 sec. Centrifuge briefly again (c. 1 min.).

6. Carefully aspirate all the alcohol solution with a micropipetter. Use a KimWipe to remove any alcohol from the sides of the tube. Be careful not to disturb the pellet, which may or may not be visible.

7. Air dry the pellet.

APPENDIX F: ADDRESSES AND CONTACT INFORMATION FOR COMPANIES USED DURING THIS RESEARCH

ANACHEM Ltd.

(Micropipette tips [racked])

20 Charles Street,

Luton,

Beds.,

LU2 OEB

tel. 01582 745000

Bioline (UK) Ltd.

(*taq* polymerase; primers)

16 The Edge Business Centre

Humber Road,

London

NW2 6EW

tel. 0181 830 5300

Web Site: http://www.bioline.com

Fisons Scientific Equipment

(Polycarbonate microcentrifuge tube box)

Bishop Meadow Road,

Loughborough,

Leicestershire,

LE11 ORG

tel. 01509 231166

Pharmacia Biotech Ltd.

(4 × 25 µmol dNTP set)

23 Grosvenor Road,

St. Albans, Hertfordshire,

AL1 3AW

tel. 01727 814000

Promega Ltd.

(Taq DNA polymerase; Wizard PCR Preps DNA Purification System)

Delta House,

Enterprise Rd.,

Chilworth Research Centre,

Southampton, SO16 7NS

tel. 0800 378994

Qiagen Ltd.

(QIAQUICK PCR purification kit)

Boundary Court,

Gatwick Road,

Crawley,

West Sussex,

RH10 2AX

tel. 01293 422 999

Web Site: http://www.qiagen.com

`Scotlab Ltd.

(Gel comb)

Kirkshaws Rd.,

Coatbridge,

Strathclyde,

ML5 5AD

tel. 01236 449330

Sigma-Aldrich Company Ltd.

(Dimethyl Sulfoxide (DMSO); Bovine Serum Albumin (BSA), Acetylated - lyophilized powder)

Fancy Road,

Poole,

Dorset, BH12 4QH

tel. 0800 373731

APPENDIX G: LARGE SCALE DNA EXTRACTION

(METHOD ADAPTED FROM DOYLE & DOYLE, 1987)

1. Preheat 5 mL CTAB and 10 µl 2-mercaptoethanol per sample at 60°C. It is wise to pre-heat more buffer than is required in case some of the samples require dilution.

Therefore for 4 samples use 30ml CTAB and 60 µl 2-mercaptoethanol.

PUT ISOPROPANOL IN THE THE FREEZER

2. Grind the leaf with a pinch of acid treated sand in a pestle with liquid nitrogen. Make sure the material is thoroughly ground into a fine powder, then add 0.5 mL volume of PVPP powder into the pestle and mix.

3. Scrape the powder into a blue top top tube and 5 mL of the preheated buffer, and mix gently, avoid leaving the dry material around the rim of the tube.

4. Incubate for 30 minutes at 60°C, shaking every 10 minutes.

5. Add an equal volume of chloroform isoamyl alcohol (24:1), mix by shaking for 40 minutes, transfer to polypropylene tubes (as the chloroform dissolves plastic), balance the tubes using chloroform isoamyl alcohol, remove the tops and cover with parafilm, spin at 10 000 rpm for 10 minutes (LARGE CENTRIFUGE).

6. Remove the supernatant with a wide-bore pastette (cut off blue tip), and repeat the chloroform extraction, this time mixing for 10 minutes.

7. Take the supernatant and transfer to a blue top tube using the wide-bore pastette. Precipitate the DNA by adding 2/3 volume freezer cold isopropanol and rocking gently. If the DNA is not spoolable, leave the tube in the freezer for about an hour (or overnight). The DNA can be left overnight at this stage if required.

8. Spool out the DNA using a glass pippette (with a heat sealed end). If the DNA is not spoolable, spin at 3000 rpm for 5 minutes (bench top centrifuge). Allow any excess liquid to air dry then transfer to 5 mL wash buffer for at least 20 minutes.Rock the tube gently to dislodge the pellet but don't try too hard!

This is the best stage to leave the DNA overnight, ie. in wash buffer.

9.Spin the DNA in wash buffer at 3000 rpm for 5 min. Remove the wash buffer and invert the tube on blue tissue to air dry the DNA. Alternatively the pellet can be picked up with a glass rod and air dryed more quickly.

10. Transfer the pellet to 1 mL of TE to resuspend it. If the pellet will not resuspend immediately, it can be left overnight to dissolve. Furthermore the addition of an extra 2 mL of TE and / or gently heating (c. 65°C water bath) may help.

PUT THE ETHANOL IN THE FREEZER

11. Add 1 µl 10 mg / mL RNAse to each 1 mL TE / DNA mixture and incubate for 60 minutes at 37°C. (Use incubator)

12. Dilute with 2 volumes TE (if only 1 mL was added at step 10) and add 0.3 mL of 3M Sodium acetate (pH 8). Mix thoroughly until the solution is homogeneous. Then add 2.5 volumes of freezer cold ethanol, and rock gently to precipitate the DNA. Keep rocking the tube until the DNA does not fall rapidly to the base of the tube.

Leave the tube in the freezer for at least 1 hour (overnight) to maximise the DNA precipitation. Leave for at least 2 weeks if extracting from herbarium material.

13. Respin the DNA at 3000 rpm for 5 minutes, remove the ethanol and air dry until can't smell the ethanol. Resuspend in 0.5-1 mL of TE or water (for PCR).

14. Check concentrations of DNA by running out 5 µL of sample against a DNA concentration standard on an agarose gel (1-1.6%).

Reagents:

CTAB Buffer

2% CTAB

20 mM EDTA

100 MM Tris-HCl pH 8.0

1.4 M NaCl

+ 0.2% β-mercaptoethanol (add just before use)

Wash Buffer

76% Ethanol

10 mM Ammonium acetate

PVPP (Polyvinyl polypyrrolidone)

Keep 0.5 mL volumes in eppendorf tubes.

APPENDIX H: MICRO-PREP DNA EXTRACTION PROTOCOL

1. Preheat 400 µL CTAB and 0.8 µL 2β-mercaptoethanol per sample at 60°C. Remove leaf material and store in liquid nitrogen.

2. Place 1 cm^2 leaf material into a 1.5 mL eppendorf tube and add 400 µL of the preheated buffer with a pinch of acid washed sand.

3. Homogenise using a sterile ground glass rod attached to a domestic power drill.

4. Add a pinch of PVPP and incubate for 30 mins at 60°C.

5. Add 400 µL of chloroform isoamyl alcohol (24:1) and shake gently for 40 mins.

6. Spin down samples at 8000 g for 10 mins.

7. Gently remove the supernatant with a medium-bore pipette tip (yellow tip) and repeat chloroform extraction, this time mixing for 20 mins.

8. Take the supernatant and transfer to another 1.5 mL eppendorf tube. Precipitate DNA by adding 2/3 volume freezer cold isopropanol and leave at -20°C overnight.

9. Spin down at 8000 g for 10 mins. Pour off overlying liquid, invert the tube and leave the pellet to air dry for 30 mins.

10. Add 200 µL of wash buffer and leave for 2-3 hours, mixing gently at 15 min intervals.

11. Spin down sample at 8000 g for 10 mins. Pour off overlying liquid, invert the tube and leave the pellet to dry for 1-2 hours.

12. Resuspend the pellet in 300 µL of TE.

13. Check concentration of DNA by running 5 μL of sample against a DNA standard on an agarose gel (1-1.6%). Store at -20°C.

APPENDIX I PURIFICATION OF PCR PRODUCTS

USING PROMEGA WIZARD PCR PREPS DNA PURIFICATION SYSTEM, CAT # A7170

Requirements:

Container to collect slurry in (c. 3.5 ml / sample)

2 x the number of samples of 1.5 ml epindorff tubes

Note: if purifying large DNA fragments, **preheat TE buffer:- >3Kb 65°-80°** C; >20Kb 80° C.

Note: Go from steps 2 - **4** quite quickly as the DNA precipitates and prevents pipetting.

1. Attach Promega Luer-Lok syringe barrel to minicolumn and take plunger from a 2ml syringe; number all epindorff tubes

2. Add 100µl Direct Purification Buffer to 30-300µl PCR product (supplement with TE if necessary) in a labelled 1.5 ml epindorff tube. Vortex briefly.

3. Add 1ml of Resin and vortex briefly 3x in 1 minute.

4. Pipet Resin/DNA mix into Syringe barrel. Insert plunger and gently push mix into minicolumn. Collect any slurry in waste container.

5. Detach the syringe from minicolumn and remove plunger. Reattach syringe barrel to minicolumn. The minicolumn and syringe can now be supported by the original epindorff tube. Pipet 2ml of 80% isopropanol into syringe and gently push through minicolumn into waste container.

6. Remove syringe, transfer minicolumn to 1.5 ml epindorff tube. Centrifuge (balance with 300µl tube if necessary) at 12000 x g for 20 sec. to dry the resin.

7. Transfer minicolumn to new epi tube, add 50µl TE (at c. 70° C for 3Kb). Wait 1 minute (the DNA will remain intact for up to 30 minutes). Centrifuge the minicolumn for 20 sec at 12 000 x g to elute the DNA.

8. Remove & discard the minicolumn.

9. Run out 5µl of purified PCR product on an agarose gel (1-1.6 %) to test for DNA.

USING QIAGEN QIAQUICK PCR PURIFICATION SYSTEM, CAT # 28104 [50] OR 28106 [250]

This protocol is designed to purify single- or double-stranded PCR products ranging from 100 bp to 10 kb from primers, nucleotides, polymerases and salts using the QIAquick spin columns in a microcentrifuge.

Notes: Add ethanol (96-100%) to Buffer PE before use (see bottle label for volume).

All centrifuge steps are at ≥ 10 000 × g (~ 13 000 rpm) in a conventional tabletop microcentrifuge.

1. Add 5 volumes of Buffer PB to 1 volume of the PCR reaction and mix. It is not necessary to remove mineral oil (but I do).
2. Place a QIAquick spin column in a provided 2-ml collection tube.
3. To bind DNA, apply the sample to the QIAquick column and centrifuge 60 sec.
4. Discard the flow-through. Place the QIAquick column back into the same tube.
5. To wash, add 0.75 ml Buffer PE to column and centrifuge for 60 sec.
6. Discard the flow-through and dry sides of tube with a tissue. Place QIAquick column back in the same tube. Centrifuge column for an additional 1 min at maximum speed.
7. Place QIAquick column in a clean 1.5 ml microfuge tube.
8. To elute DNA, add 50 µl Buffer EB (10mM Tris-Cl, pH 8.5), TE (10 mM Tris-Cl, 1mM EDTA, pH 8.0) or H_2O to the center of the QIAquick column and centrifuge for 1 min. Alternatively, for increased DNA concentration, add 30 µl elution buffer

to the center of the QIAquick column, let stand for 1 min, and then centrifuge. [I used H_2O as TE may inhibit subsequent enzymatic reaction.]

APPENDIX J USEFUL INFORMATION AND SOURCES OF INFORMATION FOR DESIGNING PRIMERS

The information in paragraphs 1-5 is taken from Palumbi (1996, p. 212-215) while paragraph 6 is a summary of information gleaned from R. Griffiths (pers. comm.) and my own experience.

1. PRIMER LENGTH

- usually sufficient with 18-24 bases
- the longer the primer, the higher the annealing temperature can be and the greater the specificity
- long primers have greater amounts of non-specific primer products present in the primer mixture

2. NUCLEOTIDE COMPOSITION

- can be any sequence
- ideally roughly equal numbers of each nucleotide without internal repeats or self similarity; otherwise may lead to self-priming and primer-dimer products
- GC rich primers can withstand higher annealing temperatures but subject to greater amounts of self-annealing

3. PRIMER-TEMPLATE MATCH

- specificity obtained through maximising sequence similarity between the primer and template
- single internal mismatches have little effect on PCR product yield when the primers are long and there are 6-10 matched bases on either side of the mismatch

- single mismatches at or near the 3' end of the primer can significantly decrease amplification
- mismatches of A:G; G:A; C:C at 3' end reduce yield c. 100 fold
- mismatches of A:A at 3' end reduce yields 20-fold
- T's appear to base pair with all 3 other bases
- very important to get good match at 3' end
- primers usually ended at second codon position
- primer enhanced if third codon position closest to the 3' end usually with 3 bases of the 3' end, is a 2-fold position or is degenerate

4. COMMON MODIFICATIONS TO PRIMERS

- restriction sites can be incorporated into the primers thus allowing easier clong of PCR products
- some suggest adding 3-5 bases to the 5' end of the primer (after the restriction site) because this increases the efficiency of digestion
- incorporation of a biotynylated nucleotide to the 5' end during primer synthesis allows solid-phase sequencing and non-isotopic detection of amplified products
- fluorescent tags can be added to nucleotides; these form the basis of detection systems in many automatic DNA sequencers

5. DESIGN OF UNIVERSAL PRIMERS

- use of degenerate primers can increase the chance of exact match of a target sequence but decrease the concentration of the exact primer and judging the best concentration of primer to use difficult

- to reduce primer degeneracy you can take advantage of ability of some mismatched base pairs to form a partial bond
- although G binds to C best, G-T bonds can also form
- for primers on the coding strand, can use G in every position in which there is a potential for either an A or G in the template
- similarity can use T in each position that has a T or a C in the template
- after a universal primer designed and used successfully it is often a good idea to design a new set of primers that work well only on the particulaaar taxon under study - typically located just inside the universal set and tend to provide more consistent amplification

6. PRACTICAL ASPECTS

- It is a really good idea to design primers with very similar 'Tm's (melting temperatures) so that they can be used for PCR reactions
- If the primer is for sequencing then the difference in Tm is not so important but it is more useful to have primers which can be used for PCR amplifications too
- Find primers with 'g' or 'c' near 3' end so that they will anneal well but try to have 'a; or 't' there too so that the binding is not too strong otherwise the primer will bind strongly to other regions with that c.g. ccg sequence
- To match the Tms alter the optimum Tm and min and max Tms to coincide with the known Tm of your original primer.

APPENDIX K *TRNC-TRND* DATA SET

```
[                          10        20        30        40        50        60        70        80]
[5'                  trnD→ .         .         .         .         .         .         .       3'.]

B. acerifolia              GCGTTCGAGC CCCGTCAGTC CCGACGCGCA TCCAAATACA ATCAAAATAG ATATATCAAT TCATCTCTTA CTTTATTGCA
B. convolvulacea           TGGT?CGAGC CCCGTCAGTC CCGACACGGA TCCAAATACT ATCAAAATAG ATATATCAAT TCATCTCTTA CTTTATTGCA
B. dipetala                ?GGTTCGAGC CCCGTCATTC CCGACACGGA TCCAAATCCA ATCAAAATAG ATATATCTAT TCATCTCTTA CTTTATTGCA
B. dregei                  GGGTTCGAGC CCCGTCAGTC CCGACACGGA TCCAAATCCA ATCAAAATAG ATATATCAAT TAATCTCTTA CTTTATTGGA
B. floccifera              GGGTTCGAGC CCCGTCAGTC CCGACACGGA TCCAAATCCA ATCAAAATAG ATATATCAAT TCATCTCTTA CTTTATTGGA
B. goegoensis              GGGTCCGAGC CCCGTCAGTC CCGACACGGA TCCAAATCCA ATCAAAATAG ATATATCAAT TCATCTCTTA CTTTATTTGA
B. gracilis                GGGTTCGAGC CCCGTCAGTC CCGACACGGA TCCAAATCCA ATCAAAATAG ATATATCAAT TCATCTCTTA CTTTATTGGA
B. cf. grandis             TGGTGCGAGC CCCGTCAGTC CCGACACGGA TCC???TCC? ?TC??A?TAG ATATATCAAT TCATCTCGTA CTTTATTGGA
B. grandis                 ?GGT?CGAGC CCCGTCAGTC CCGAC?CGGA TCC??ATCC? ?CCAA??TAG ATATATCAAT TCATCTCGTA CTTTATTGGA
B. heracleifolia           GGGTTCGAGC CCCGTCAGTC CCGACACGGA TCCAAATCCA ATCAAAATAG ATATATCAAT TCATCTCTTA CTTTATTGGA
B. incarnata               ---------- ---------- ---------- ---------- ---------- -----TCA?T TCATCTCTTA CTTTATTGGA
B. malachosticta           ?GGTTCGAGC CCCGTCAGTC CCGACACGGA TCCAAATCCA ATCAAAATAG ATATATCAAT TCATCTCTTA CTTTATTTGA
B. mannii                  ?GGTTCGAGC CCCGTCATTC CCGACAC?GA TCCAAATCCA ATCAAAATAG ATATATCAAT TCATCTTTTA CTTTATTGTA
B. masoniana               GGGTTCGAGC CCCGTCAGTC CCGACACGGA TCCAAATCCA ATCAAAATAG ATATATCAAT ---------- ----------
B. maynensis               GGGT?CGACC CCCGTCAGTC CCGACATGGA TCCAAATCCA ATCAAAATA? ATATATCAAT TCATCTCTTA CTTTATTGGA
B. meyeri johannis         GGGTTCGACC CCCGCCAGTC CCGACACGGA TCCAAATCCA ATCAAAATAG ATATATCAAT TCATCTTCTA CTTTATTGTA
B. oaxacana                GGGTTCGAGC CCCGTCAGTC CCGACACGGA TCCAAATCCA ATCAAAATAG ATATATCAAT TCATCTCTTA CTTTATTGGA
B. obliqua                 GGGTTCGACC CCCGTCAGTC CCGACACGGA TCTAAATCCA ATCAAAATAG ATATATCAAT TCATCTCTTA CTTTATTGGA
B. olbia                   ---------- ---------- ---------- ---------- ---------- ----------T TCATCTCTTA CTT?ATTGGA
B. aff. palmata            GGGTTCGAGC CCCGTCAGTC CCGACACGGA TCCAAATCCA ATCAAAATAG ATATATCAAT TCATCTCTTA CTTTATTGGA
B. partita                 GGGTTCGACC CCCGTCAGTC CCGACACGGA TCCAAATCCA ATCAAAATAG ATATATCAAT TAATCTCTTA CTTTATTGGA
B. peltata                 GGGTTCGAGC CCCGTCAGTC CCGACACGGA TCCAAATCCA ATCAAAATAG ATATATCAAT TCATCTCTTA CTTTATTGGA
B. rajah                   GGGTTCGAGC CCCGTCAGTC CCGACACGGA TCCAAATCCA ATCAAAATAG ATATATCAAT TCATCTCTTA CTTTATTTGA
B. ravenii                 GGGTTCGAGC CCCGTCAGTC CCGAC?CGGA TCCAAATCCA ATCAAAATAG ATATATCAAT TCATCTCTTA CTTTATTGGA
B. roxburghii              ---------- ---------- ---------- ---------- ---------- ---------- -CATCTCTTA CTT?ATTGGA
B. rubella                 GGGTTCGAGC CCCGTCAGTC CCGACACGGA TCCAAATCCA ATCAAAATCG ATATATCAAT TCATCTCTTA CTTTATTGGA
B. salaziensis             ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. sutherlandii            ---------- ---------- ---------- ---------- ---------- ---------- ----CTCT?? CTTTATTGGA
B. tayabensis              GGGTTCGAGC CCCGTCAGTC CCGACACGGA TCCAAATCCA ATCAAAATAG ATATATCAAT TCATCTCTTA CTTTATTTGA
B. ulmifolia               GGGTTCGAGC CCCGTCAGTC CCGACACGGA TCA?AATCCA ATCAAAATAG ATATATCAAT TCATCTCTTA CTTTATTGCA
B. wollnyi                 ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
Datisca                    ---------- ---------- ---------- ---------- ---------- ----ATCAAT TCATCTCT?C ?GGGACTGTC
Symbegonia sanguinea       GGGTTCGAGC CCCGTCAGTC CCGACACGGA TCCAAATCCA ATCAAAATAG ATATATCAAT TCATCTCTTA CTTTATTTGA
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APPENDIX K CONTD.

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[                    90         100        110        120        130        140        150        160]
[                     .          .          .          .          .          .          .          .]

B. acerifolia        AAAG-AAAGA ACAAATAACA TAA-----TT TT-------- -TGGCTCTTT CTTATTT--- ---TATAGTT TTTATATTTT
B. convolvulacea     AAAG-AAAGA ACAAATAACA TAACATAATT TT-------- -TGGCTCTTT CTTATTT--- ---TATAGTT TTTATATTTT
B. dipetala          AAAG-AGAGA ACAAATAACA TAACAGAATT TT-------- -CGGATCTTT CTTGTTT--- ---TATAGTT TTTATATTTG
B. dregei            AAAG-AGAGA ACAAATAACA TAACAGAATT TT-------- -CGGATCTTT CTTGTTT--- ---TATAGT? TTTATATTTT
B. floccifera        AAAG-AGAGA ACAAATAACA TAACAGAATT TC-------- -CGGATCTTT CTTGTTT--- ---TATAGTT TTGATATTTT
B. goegoensis        AAAG-AGAGA ACAAATAACA TAACAGAATT TT-------- -CGGATCTTT CTTGTTT--- ---TATAGTT TTTATATTTT
B. gracilis          AAAG-AGAGA ACAAATAACA TAACAGAATT TT-------- -CGGATCTTT CTTGTTT--- ---TATAGTT TTTATATTTT
B. cf. grandis       AAAG-ACAGA ACAAATAACA TAATAGAATT TT-------- -AGGATC--- ---------- ---TATAGTT TTTATATTTT
B. grandis           AAAG-AGAGA ACAAATAACA TAATAGAATT TT-------- -AGGATC--- ---------- ---TATAGTT TTTATATTTT
B. heracleifolia     AAAG-AGAGA ACAAATAACA TAACAGAATT TT-------- -CGGATCTTT CTTGTTT--- ---TATAGTT TTAATATTTT
B. incarnata         AAAG-AGAGA ACAAAT?ACA T??CAGAATT TT-------- -CGGATCTTT CTTGTTTTTG T?TTATAGTT TT?ATATTTT
B. malachosticta     AAAG-AGAGA ACAAATAACA TAACAAAATT TT-------- -CGGATCTTT CTTGTTT--- ---TATAGTT TTTATATTTG
B. mannii            AAAG-AGAGA ACAAATAACA TAACAGAATT TT-------- -CGGATCTTT CTTCTTT--- ---TATATTT TTTATATTTT
B. masoniana         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. maynensis         AAAG-AGAGA ACAAATTAC? TAACAGAATT TT-------- -CGGATCTTT CTTGTTT--- ---TATAGTT TTCATATTTT
B. meyeri johannis   AAAG-AGAGA ACAAATAGCA TAACATAATT TT-------- -CGGATCTTT CTTTTTT--- ---------- ---ATATTTT
B. oaxacana          AAAG-AGAGA ACAAATAACA TAA-----TT TT-------- -TG-ATCTTT CTTGTTT--- ---TATAGTT TTTATATTTT
B. obliqua           AAAG-AAAGA ACAAATAACA TAACAGAATT TT-------- -TGGATTTTT CTTGTTT--- ---TATAGTT TTTATATTTT
B. olbia             AAAG-AGAGA ACAAATAACA TAACAGAATT TT-------- -CGGATCTTT ATTGTTT--- ---TATAGTT TTTATATTTT
B. aff. palmata      AAAG-AGAGA ACAAATAACA TAACAGAATT TT-------- -CGGATCTTT CTTGTCT--- ---TATAGTT TTTATATTTT
B. partita           AAAG-AGAGA ACAAATAACA TAACAGAATT TT-------- -CGGATCTTT CTTGTCT--- ---TATAGTT TTTATATTTT
B. peltata           AAAG-AGAGA ACAAATAACA TAACAGAATT TT-------- -CGGATCTTT CTTGTCT--- ---TATAGTT TTTATATTTT
B. rajah             AAAG-AGAGA ACAAATAACA TAACAGAATT TT-------- -CGGATCTTT CTTGTCT--- ---TATAGTT TTTATATTTT
B. ravenii           AAAG-AGAGA ACAAATAACA TAACAGAATT TT-------- -CGGATCTTT CTTGTCT--- ---TATAGTT TTTATATTTT
B. roxburghii        AAA?-AGAGA ACAAATAACA TAACAGAATT T?-------- -CGGATCTTT CTTGTTT--- ---TATAGTT T??ATATTTC
B. rubella           AAAG-AGAGA ACAAATAACA TAACAGAATT TT-------- -CGGATCTTT CTTGTTT--- ---TATAGTT TTTATATTTT
B. salaziensis       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. sutherlandii      AAAG-AGAGA AC???TAACA T????GAATT TT-------- -CGGATCTTT CTTGTTT--- ---TATAGTT TTTATATTTT
B. tayabensis        AAAG-AGAGA ACAAATAACA TAACAGAATT TT-------- -CGGATCTTT CTTGTTT--- ---TATAGTT TTTATATTTT
B. ulmifolia         AAAG-AAAGA ACAAATAACA TAACATAATT TT-------- -TGCCTCTTT CTTATTT--- ---TATAGTT TTTATATTTT
B. wollnyi           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
Datisca              AATGGAGAGA AGGAAGAATA T??CA?A?TT TTACTCCAAA TGGGATCCCT TTTTTTT--- ---TTTTTTT CTTTTCAAAT
Symbegonia sanguinea AAAG-AGAGA ACAAATAACA TAACAGAATT TT-------- -CGGATCTTT CTTGTTT--- ---TATAGTT TTTATATTTT
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APPENDIX K CONTD.

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[                 170        180        190        200        210        220        230        240]
[                  .          .          .          .          .          .          .          .]

B. acerifolia     ATTT-----T TTCACATTTT AAATG----- --AAACAAAA TAAATCTGGA AATTTTCAGT TTTTCAACAA GTACTTTTTC
B. convolvulacea  ATTT-----T TTCACATTTT AAATG----- --AAACAAAA TAAATCTGGA AATTTTCAGT TTTTCAAGAA GTACTTTTTC
B. dipetala       ATTTCATTTT TTCACATTTA TTATG----- --AAACCAAA CAAATCTGGA AATTTCCAGT TCTTCAAGAA GTACTTTTTC
B. dregei         ATTT-----? TTCACATTTA TTATG----- --AAACCAAA CAAATCTGGA AATTTGCAGT TCTTCAAGAA GTACTTTTTC
B. floccifera     ATTT-----T TTCACATTTA TTATGTATTA TGAAACCAAA CAAATCTGGA AATTTGCAGT TCTTCAAGAA GTACTTTTTC
B. goegoensis     ATTT-----T TTCACATTTA TTATG----- --AAACCAAA CAAATCTGGA AATTTGCAGT TCTTCAAGAA GTACTTTTTC
B. gracilis       ATTT-----T TTCACAGTTA TTATG----- --AAACAAAA AAAATCTGCA AATTTGAAGT TCTTCAAGAA GTACTTTTTC
B. cf. grandis    CTTT-----T TTCACATTTA TTATG----- --AAACCAAA CAAATCTGCA AATTTTCAGT TCTTCAAGAA GTACTTTTTC
B. grandis        CTTT-----T TTCACATTTA TTATG----- --AAACCAAA CAAATCTGGA AATTTTCAGT TCTTCAAGAA GTACTTTTTC
B. heracleifolia  CTTT-----T TTCACATTTA TTATG----- --AAACCAAA CAAATCTGGA AATTTGAAGT TCTTCAAGAA GTACTTTTTC
B. incarnata      ATTT-----T TTCACATTTA TTATG----- --AAACCAAA CAAATCTGGA AATTTTAAGT TCTTCAATAA GTACTTTTTC
B. malachosticta  ATTT-----T TTCACATTTA TTATG----- --AAACCAAA CAAATCTGGA AATTTTCAGT TCTTCAAGAA GTACTTTTTC
B. mannii         ATTT-----T TTCACATTTA TTATC----- --AAACCAAA CAAATCTGGA AATTTTCAGT TCTTCAACAA GTACTTATTC
B. masoniana      ---------- ---------- ---------- ---------- ---------- ---------- -----AAGAA GTACTTTTTC
B. maynensis      ATTT-----T TTCACATTTA TTATG----- --AAACCAAA CAAATCTGGA AATTT?AAGT TCTTC?AGAA GTACTTT??C
B. meyeri johannis CTTT-----T TTCACATTTC TTATC----- --AAACCAAA CAAATCTGGA AATTTGCAGT TCTTCAAGAA GTACTTATTC
B. oaxacana       ATTT-----T TTCACATTTA TTATG----- --AAACCAAA CAAATCTGGA AATTTTTAGT TCTTCAAGAA GTACTTTT?C
B. obliqua        CTTT-----T TTCACATTTA TTCTG----- --AAACCAAA CAAATCTGGA AATTTGCAGT TCTTCAAGAA GTACTTTTTC
B. olbia          CTTT-----T TTCACATTTA TTATG----- --AAACCAAA CAAATCTGGA AATTTTCAGT TCTTCAAGAA GTACTTTTTC
B. aff. palmata   ATTT-----T TTCACATTTA TTATG----- --AAACCAAA CAAATCTGGA AATTTGCAAT TCTTTAAGAA GTACTTTTTC
B. partita        ATTT-----T TTCACATTTA TTATG----- --AAACCAAA CAAATCTGGA AATTTGCAGT TCTTCAAGAA GTACTTTTTC
B. peltata        ATTT-----T TTCACATTTA TTATG----- --AAACCAAA CAAATCTGGA AATTTGAAGT TCTTCAAGAA GTACTTTTTC
B. rajah          ATTT-----T TTCACATTTA TTATG----- --AAACCAAA CAAATCTGGA AATTTGCAGT TCTTCAAGAA GTACTTTTTC
B. ravenii        ATTT-----T TTCACATTTA TTATG----- --AAACCAAA CAAATCTGGA AATTTGCAAT TCTTCAAGAA GTACTTTTTC
B. roxburghii     ---------- --CACATTTA TTATG----- --AAACCAAA CAAATCTGGA AATTTGCAAT TCTTCAAGAA GTACTTTTTC
B. rubella        ATTT-----T TTCACATTTA TTATG----- --AAACCAAA CAAATCTGGA AATTTGCAGT TCCTCAAGAA GTGCTTTTTC
B. salaziensis    ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. sutherlandii   ATTT-----T T?CACATTTA TTATG----- --AAACCAAA CAAATCTGGA AATTTGCAGT TCTTCAAGAA GTACTTTTTC
B. tayabensis     ATTT-----T TTCACATTTA TTATG----- --AAACTAAA CAAATCTGGA AATTTGCAGT TCTTCAAGAA GTACTTTTTC
B. ulmifolia      ATTT-----T TTCACATTTA AAATG----- --AAACAAAA TAAATCTGGA AATTTTCAGT TTTTCAAGAA GTACTTTTTC
B. wollnyi        ---------- --CACATTTA TTATG----- --AAACCAAA CAAATCTGGA AATTTTCAGT TCTTCAAGAA GTACTTTTTC
Datisca           TTCT-----C ATCAAAT--- ---------- -----CCAA- CAAATATGGG AATTTCCATT TCTTCAACAA GTACTGATTG
Symbegonia sanguinea ATTT-----T TTCACATTTA TTATG----- --AAACCAAA CAAATCTGGA AATTTTCAGT TCTTCAAGAA ATACTTTTTC
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APPENDIX K CONTD.

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[                                250       260       270       280       290       300       310       320]
[                                 .         .      BEG-TRND2-F------------------------------>
                                                                DAT-TRND-B<-------------------------------
                                                                                    DAT-TRND2-F------------
B. acerifolia                    ATGGGAGAAA GGCATATGTA GATTAGTACA ATTATTGGTA AAATAATATT CAGGATTCAA ACAATAGATA CCAGAATGGA
B. convolvulacea                 ATGGGAGAAA GGCATATGTA GATTAGTACA ATTATTGGTA AAATCATATT CAGGATTCAA ACAATAGATA CCAGAATGGA
B. dipetala                      ATGGGAGAAA GGCATATGTA AATTAGTACA ATTATTGGTA GAATCATATT CAGGATTCAA ACAATAGATA CCAGAATGGG
B. dregei                        ATGGGAGAAA GGCATATGTA GATTAGTACA ATTATTGCTA GAATCATATT CAGCATTCAA ACAATAGATA CCA?AATGGG
B. floccifera                    ATGGGAGAAA GGCATATGTA GATTAGTACA ATTATTGGTA GAATTATATT CAGGATTCAA ACAATAGATA CCAGAATGGG
B. goegoensis                    ATGGGAGAAA GGCATATGTA GATTAGTACA ATTATTGGTA GAATCATATT CAGGATTCAA ACAATAGATA CCAGAATGGG
B. gracilis                      ATGGGAGAAA GACATATGTA GATTAGTACA ATTATTGCTA GAATCATATT CAGGATTCAA ACAATAGATA CCAGAATGGG
B. cf. grandis                   ATGGGAGAAA GGCATATGTA GATTAGTACA ATTATTGGTA GAATCAGATT CAGGATTCAA ACAATAGATA CCAGAATGGG
B. grandis                       ATGGGAGAAA GGCATATGTA GATTAGTACA ATTATTGGTA GAATCAGATT CAGGATTCAA ACAATAGATA CCAGAATGGG
B. heracleifolia                 ATGGGAGAAA GGCATATGTA GATTAGTACA ATTATTGCTA GAATCATATT CAGGATTCAA ACAATAGATA CCAGAATGGG
B. incarnata                     ATGGGAGAAA GGCATATGTA GATTAGTACA ATTATTGCTA GAATCATATT CAGGATTCAA ACAATAGATA CCAGAA----
B. malachosticta                 ATGGGAGAAA GGCATATGTT TATTAGTACA ATTATTGGTA GAATCATATT CAGGATTCAA ACAATAGATA CCACAATGGG
B. mannii                        ATGGCAGAAA GGCATATGTA AATTAGTACA ATTATTGGTA GAATAATATT CAGGATTCAA ACAATACATA CCAGAATGGT
B. masoniana                     ATGGGAGAAA GGCATATGTG GATTAGTACA ATTATTGGTA GAATCATATT CAGGATTCAA ACAATAGATA CCAGAATGGG
B. maynensis                     ATGGGAGAAA GGCATATGTA GATTAGTACA ATTATTGATA GAATCATATT CAGGATTCAA ACAATAGATA CCAGAATGGG
B. meyeri johannis               ATGGGAGAAA GGCATATGTA GATTAGGACA ATTATTGGTA GAATCATATT CAGGATTCAA ACAATAGATA CCAGAATGGG
B. oaxacana                      ATGGGAGAAA GGCATATGTA GAT?AGTACA ATTATTGCTA GAATCCTATT CACGATTCAA ACAATAGATA CCAGAATGGG
B. obliqua                       ATGGCAGAAA GTCATATGTA GATTAGTACA ATTATTGCTA GAATCATATT CAGGATTCAA ACAATAGATA CCAGAATGGG
B. olbia                         ATGGGAGAAA GGCATATGTA GATTAGTACA ATTATTGGTA GAATCATATT CAGGATTCAA ACAATAGATA CCAGAATGGA
B. aff. palmata                  ATGGGATAAA GGCATATGTA GATTAGTACA ATTATTGGTA GAATCATATT CAGGATTCAA ACAATAGATA CCAGAATGGG
B. partita                       ATGGGAGAAA GGCATATGTA GATTAGTACA ATTATTGCTA GAATCATATT CAGGATTCAA ACAATAGATA CCAGAATGGC
B. peltata                       ATGGGAGAAA GGCATATGTA ?ATTA?TACA ATTATTG?TA ?AATC?T?TT CAGCATTCCA AC?ATAGATA CCAGAATGGG
B. rajah                         ATGGGAGAAA GGCATATGTA GATTAGTACA ATTATTGGTA GAATCATATT CAGGATTCAA ACAATAGATA CCAGAATGGG
B. ravenii                       ATGGGATAAA GGCATATGTA GATTAGTACA ATTATTGCTA GAATCATATT CAGGATTCAA ACAATAGATA CCAGAATGGG
B. roxburghii                    ATGGGATAAA GGCATATGTA ?ATTAGTACA ATTATTGGTA GAATCATATT CAGGATTCAA ACAATAGATA CCACAATGGG
B. rubella                       ATGGGATAAA GGCATATGTA GATTAGTACA ATTATTGGTA GAATCATATT CAGGATTCAA ACAATAGATA CCAGAATGGG
B. salaziensis                   ---------- ---------- ---------- ---------- ---------- ---------- ---------- ---GAATGGG
B. sutherlandii                  ATGGGAGAAA GGCATATGTA GATTAGTACA ATTATTGCTA GAATCATATT CAGGATTCAA ACAATAGATA CCAGAATGGG
B. tayabensis                    ATGGGAGAAA GGCATATGTA GATTAGTACA ATTATTGGTA GAATCCTATT CACGATTCAA ACAATAGATA CCAGAATCGG
B. ulmifolia                     ATGGGAGAAA GGCATATGTA GATTAGTACA ATTATTGGTA AAATCATATT CAGGATTCAA ACAATAGATA CCAGAATGTA
B. wollnyi                       ATGGGAGAAA GGCATATGTA GATTAGTACA ATTATTGCTA GAATCATATT CAGGATTCAA ACAATAGATA CCAGAATGGG
Datisca                          ATGGGAGAAA CACATATGTG GATTAGTACA ATTATTGGTA GAAAAATATT CAGGATTCCA AGG---GATA CCATACCGGG
Symbegonia sanguinea             ATGGGAGAAA GGCATATGTA GATTAGTACA ATTATTGGTA GAATCATATT CAGGATTCAA ACAATAGATA CCAGAATGGG
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APPENDIX K CONTD.

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[                                  330         340         350         360         370         380         390         400]
[                                   .           .           .           .           .          BEG-TRND1-R←                 ]
                DAT-TRND2-F→
B. acerifolia                      CCTGGCTTTT TGAATTATTC CCTATTTT-- ---------- --?TGAGTAC TATATGTTTC CCGGGAGCAC ATACAAAA?T
B. convolvulacea                   CCTGGCTTTT TGAATTATTC CCTATTT--- ---------- --TTGAGTAC TATATGTTTC CCGCGAGCAC ATACAAAAAT
B. dipetala                        CCTGGCTTTT TGAATTCCTC CCGATTGT-- ---------- --GGGAGTAC TATATGTTTC -GGGGAGCAC ATACAAAAAT
B. dregei                          CCTGGCTTTT TGAATTACTC CCTCTTT--- ---------- --GGGAGTAC TATATGTTTC CAGGGAGCAC ATACAAAAAT
B. floccifera                      CCTGGCTTTT TGAATTACTC CCAATTGC-- ---------- --GGGAGTAC TATATGTTTC -GGGGAGCAC ATACAAAAAT
B. goegoensis                      CCTGGCTTTT TGAATTACTC CCGATTGT-- ---------- --GGGAGTAC TATATGTTTC -GGGGACCAC ATACAAAAAT
B. gracilis                        CTTGGCTTTT TGAATTACTC CCGGTTT--- ---------- --TGGAGTAC TATATGTTTC CGGCGAGCAC ATACAAAAAT
B. cf. grandis                     CCTGGCTTTT TGAATTACTC TCGATTGT-- ---------- --GGGAGTAC TATATGTTTC -GGGGAGTAC ATACAAAAAT
B. grandis                         CCTGGCTTTT TGAATTACTC TCGATTGT-- ---------- --GGGAGTAC TATATGTTTC -GGGGAGTAC ATACAAAAAT
B. heracleifolia                   CTTGGCTTTT TGAATTACTC CCGGTTT--- ---------- --GGGAGTAC TATATGTTTC GGGGAAGCAC ATACAAAAAT
B. incarnata                       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. malachosticta                   CCTGGCTTTT TGAATTACTC CCGATTGT-- ---------- --GCGAGTAC TATATGTTTC -GGGGAGCAC ATACAAAAAT
B. mannii                          CCTGGTTT?T TGAATTACCC CCGATTGTGT AATCGAA--- --GGGAGTAC TATATGTTTT TCGGGAGCAC ATACAAAAAT
B. masoniana                       CCTGGCTTTT TGAATTACTC CCAATTGT-- ---------- --GGGAGTAC TATATGTTTC -GGGGAGCAC ATACAAAAAT
B. maynensis                       CTTGGCTTTT TGAATTACTC CCGGTTT--- -------GGG ATGGGAGTAC TATATGTTTC TGGGGAGCAC ATACAAAAAT
B. meyeri johannis                 CCTGGCTTTT TGAATTACTC CCGATTGTGT AATAGAA--- --GGGAGTAC TATATGTTTC ACGGGAGCAC ATAAAAAAAT
B. oaxacana                        CTTGGCTTTT TGAATTACTC CCGGTTT--- ---------- --GGGAGTAC TATATGTTTC CGGGGACCAC ATACAAAAAT
B. obliqua                         CTTGGCTTTT TGAATGAGTC CC--TTT--- ---------- --TGGAGTAC TATATCTTTC GGGGGAGCAC ATACAAAAAT
B. olbia                           CCTGACTTTT TGAATTACTC CCGACTGC-- ---------- --GAGAGTAC TATATGTTTC CCGGGAGCAC ATACAAAAAT
B. aff. palmata                    CCTGGCTTTT TGAATTACTT CCGATTGT-- ---------- --GGGAGTAC TATATGTTTC -GGGTAGCAC ATACAAAAAT
B. partita                         CCTGGCTTTT TGAATTACTC CCTGTTT--- ---------- --GGGAGTAC TATATGTTTC CAGGGAGCAC ATACAAAAAT
B. peltata                         CTTGGCTTTT TGAATTATTC CCGGTTT--- ---------- --GGGAGTAC TATATGTTTC GGGGGAGCAC ATACAAAAAT
B. rajah                           CCTGGCTTTT TGAATTACTC CCGATTGT-- ---------- --GGGAATAC TATATGTTTC -GGGGAGCAC ATACAAAAAT
B. ravenii                         CCTGGCTTTT TGAATTACTT CCGATTGT-- ---------- --GCGAGTAC TATATGTTTC -GGGTAGCAC ATACATAAAT
B. roxburghii                      CCTGGCTTTT TGAATTACTT CCGATTGT-- ---------- --GGGAGTAC TATATGTTTC -GGGTAGCAC ATACATAAAT
B. rubella                         CCTGGCTTTT TGAATTACTT CCGATTGT-- ---------- --GGGAGTAC TATATGTTTC -GGGTAGCAC AGAAAAAAAT
B. salaziensis                     CCTGGCTTTT TGAATTACTT CCGATTGTGT AATGGAA--- --GGGAGTAC TATATGTTTC CCGGGAGCAC ATACAAAAAT
B. sutherlandii                    CCTGGCTTTT TGAATTACTC CCGGTTT--- ---------- --GGGAGTAC TATACGTTTC CAGGGAGCAC ATACAAAAAT
B. tayabensis                      CCTGGCTTTT TGAATTACTC CCGATTGT-- ---------- --GGGAGTAC TATATGTTTC -GGGCAGCAC ATACAAAAAT
B. ulmifolia                       CCTGGCTTT? TTAATTATTC CCTTTTGT-- ---------- --TTTAGTAC TATATGTTTC CCGGGAGCAC ATACAAAAAT
B. wollnyi                         TTTGGCTTTT TGAATTACTC CCGGTTT--- ---------- --GGGAGTAC TATATTTTTC TGGGGAGCAC ATACAAAAAT
Datisca                            TCTGGCTTTT TTTTTTACTC CCGA?TGTGT AATGGAA--- --TAGAGTAC TATATGTTTT TCGGGAGAAC ATACACAAAT
Symbegonia sanguinea               CCTGGCTTTT TGAATTACTC CCGATTGT-- ---------- --AGGAGTAC TATATGTTTC -CGGGAGCAC ATACAAAAAT
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APPENDIX K CONTD.

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[                    410        420        430        440        450        460        470        480]
[                    ←──BEG-TRND1-R  .          .          .          .          .          .          .]

B. acerifolia        TCCATTT--- -GTACGATAC AAAAGAAATT T-CAC----- ---------- ATAGTTCCTT TGATAGACTT TTTC-ATATT
B. convolvulacea     TCCATTT--- -GTACGATAC AAAAGAAATT T-CAC----- ---------- ATAATTACTT TGATAGACTT TTTC-ATATT
B. dipetala          TTCATTT--- -GTACGATAC AAAATCAATT T-CAC----- ---------- ATACTTACTT TGATAGAATT TTTC-ATATT
B. dregei            TCCATTT--- TGTACGATAC AAAATCAATT T-CAC----- ---------- ATAGTTACTT TGATAGAATT TTTC-ATATT
B. floccifera        TCCATTT--- -GTACGATAC AAAATCAATT T-CAC----- ---------- ATAGTTACTT TGATAGAATT TTTC-ATATT
B. goegoensis        TCCATTT--- -GTACGATAC AAAATAAATT T-CAC----- ---------- ATAGTTACTT TGATAGAATT TTTC-ATATT
B. gracilis          TCCATTT--- -GTACGATAC AAAATAAATT T-CAC----- ---------- ATAGTTACTT TGATAGAATT TTTC-ATATT
B. cf. grandis       TCCATTT--- -GTACGATAC AAAATCAATT T-CAC----- ---------- ATAGTTACTT TGATAGAATT TTTC-ATATT
B. grandis           TCTATTT--- -GTACGATAC AAAATCAATT T-CAC----- ---------- ATAGTTCCTT TGATAGAATT TTTC-ATATT
B. heracleifolia     TCCATTT--- -GTACGATAC AAAATAAATT T-CAC----- ---------- ATAGTTACTT TGATAGAATT TTTA-ATATT
B. incarnata         ---------- ---------- ---------- ---------- ---------- ---------- ---TAGAATT TTTC-ATATT
B. malachosticta     TCCATTT--- -GTACGATAC AAAATCAATT T-CAC----- ---------- ATAGTTACTT TGATAGAATT TTTC-ATATT
B. mannii            TCCATTT--- -GTAGGATAC AAAATTAATT T-CAC----- ---------- ATAGTTACTT TGATAGAATT TTTC-ATATT
B. masoniana         TCCATTT--- -GTACGATAC AAAATCAATT T-CAC----- ---------- ATAGTTACTT TGATAGAATT TTTC-ATATT
B. maynensis         TCCATTT--- -GTACGATAT AAAAGCAATT T-CAC----- ---------- ATAGTTACTT TCATAGAATT TTTC-ATATT
B. meyeri johannis   TCCATTT--- -GTACGATAC AAAATAAATT T-CAC----- ---------- ATAGTTACTT TGATAGAATT TTTCTATATT
B. oaxacana          TCCATTT--- -GTACGATAC AAAAGAAATT T-CAC----- ---------- ATAGTTACTT TGATAGAATT TTTC------
B. obliqua           TCCATTT--- -GTACGATAC AAAATCAATT T-CAC----- ---------- ATAGTGACTT TGATAGAATT TTTC-ATATT
B. olbia             TCCATTT--- -GTACGATAC AAAATCAATT T-CAC----- ---------- ATAGTTACTT TGATAGACTT TTTC-ATATT
B. aff. palmata      TCCATTT--- -GTACGATAC AAAATCAATT T-CACCAAAA TCAATTTCAC ATAGTTACTT TGATAGAATT TTTC-ATATT
B. partita           TCCATTT--- TGTACGATAC AAAATCAATT T-CAC----- ---------- ATAGTTACTT TGATAGAATT TTTC-ATATT
B. peltata           TCCATTT--- -GTACGATAC AAAATAAATT T-CAC----- ---------- ATAGTTACTT TGATAGAATT TTTC-ATATT
B. rajah             TCCATTT--- -GTACAATAC AAAATAAATT T-CAC----- ---------- ATAGTTACTT TGATAGAATT TTTC-ATATT
B. ravenii           TCCATTT--- -GTACGATAC AAAATCAATT T-CACCAAAA TCAATTTCAC ATAGTTACTT TGATAGAATT TTTC-ATATT
B. roxburghii        TCCATTT--- -GTACGATAC AAAATCAATT T-CACCAAAA TCAATTTCAC ATAGTTACTT TGATAGAATT TTTC-ATATT
B. rubella           TCCATTT--- -GTACGATAC AAAATCAATT T-CAC----- ---------- ATAGTTACTT TGATAGAATT TTTC-ATATT
B. salaziensis       TCCATTT--- -GTATGATAC AAAATCAATT T-CAC----- ---------- ATAGTTACTT TGATAGAATT TTTC-ATATT
B. sutherlandii      TCCATTT--- -GTACGATAC AAAATCAATT T-CAC----- ---------- ATAGTTACTT TGATAGAATT TTTC-ATATT
B. tayabensis        TCCATTT--- -GTACGATAC AAAATCAATT T-CAC----- ---------- ATAGTTACTT TGATAGAATT TTTC-ATATT
B. ulmifolia         TCCATTT--- -GTACGATAC AAAAGAAATT T-CAC----- ---------- ATAGTTACTT TGATAGACTT TTTC-ATATT
B. wollnyi           TCCATTT--- -GTACGATAC AAAATCAATT T-TAC----- ---------- ATAGTTACTT TCATAGAATT TTTC-ATATT
Datisca              GGGATTTATT TGTACGATAC AAAAAAAAAT TGCAC----- ---------- ATA?TTACTT TGATA?AATT TT?C-GTCTG
Symbegonia sanguinea TCCATTT--- -GTACGATAC AAAATCAATT T-CAC----- ---------- ATAGTTACTT TGATAGAATT TTTC-ATATT
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APPENDIX K CONTD.

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[                490       500       510       520       530       540       550       560]
[                 .         .         .         .         .         .         .         .]

B. acerifolia    AAAATATCTT T--------- ---CCGATTT TGTGTAATCT CCATT----- ---------- ATTAATTCAA ATTACAAATT
B. convolvulacea AAAATATCTT T--------- ---CCGATTT TGTGTAATCT CCATT----- ---------- ATTAATTCAA ATTACAAATT
B. dipetala      AAAATATCTT T--------- ---CCGATTT TGTGTAATCT CAATT----- ---------- ATTAATTCAA ATTACGAATT
B. dregei        AAAATATCTT T--------- ---CCGATTT TGTGTAATCT CAATT----- ---------- ATTAATTAAA ATTACCAATT
B. floccifera    AAAATATCTT T--------- ---CCGATTT TGTATAATCT CAATT----- ---------- ATTAATTCAA ATTACGAATT
B. goegoensis    AAAATATCTT T--------- ---CCGATTT TGTGTAATCT CAATT----- ---------- ATTAATTCAA ATTACGAATT
B. gracilis      AAAATATCTT T--------- ---CCGATTT TGTGTAATCT CAATT----- ---------- ATTAATTCAA ATTACGAATT
B. cf. grandis   AAAATATCTT T--------- ---CCGATTT TGTGTAATCT AAATT----- ---------- ATTAATTAAA ATTACGAATT
B. grandis       AAAATATCTT T--------- ---CCGATTT TGTGTAATCT AAATT----- ---------- ATTAATTAAA ATTACGAA--
B. heracleifolia AAAATATCTT T--------- ---CCGATTT TGTGTAATCT CAATT----- ---------- ATTAATTAAA ATTACGAATT
B. incarnata     AAAATATCTT T--------- ---CCGATTT TGTGTAATCT CAATT----- ---------- ATTAATTCAA ATTACGAATT
B. malachosticta AAAATATTTT T--------- ---CCGATTT TGTGTAATCT CAATT----- ---------- ATTAATTCAA ATTACGAATT
B. mannii        CAAATATCTT TTCTTT---- ---CCGATTT TGTGTAATCT CAATT----- ---------- ATTAATTAAA ATTACGAATT
B. masoniana     AAAATATCTT T--------- ---CCGATTT TGTGTAATCT CAATT----- ---------- ATTAATTCAA ATTACGAATT
B. maynensis     AAAATATCTT T--------- ---CCGATTT TGTGTAATCT AAATT----- ---------- ATTAATTCAA ATTACGAATT
B. meyeri johannis AAAATATCTT T--------- ---CCGATTT TGTGTAATCT CAATT----- ---------- ATTAATTCAA ATTATGAATT
B. oaxacana      ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. obliqua       CAAATATCTT T--------- ---CCTATTT TGTGTAATAT CAACT----- ---------- ATTAATTCAA ATTACGAATT
B. olbia         AAAATATCTT T--------- ---CCGATTT TGTGTAATCT CAATT----- ---------- ATTAATTCAA ATTACGAATT
B. aff. palmata  AAAATATCTT T--------- ---CCGATTT TGTGTAATCT AAATT----- ---------- ATTAATTAAA ATTACGAATT
B. partita       AAAATATCTT T--------- ---CCGATTT TGTGTAATCT CAATT----- ---------- ATTAATTAAA ATTACGAATT
B. peltata       AAAATATCTT T--------- ---CCGATTT TGTGTAATCT CAATT----- ---------- ATTAATTAAA ATTACGAATT
B. rajah         AAAATATCTT T--------- ---CCGATTT TGTGTAATCT CAATT----- ---------- ATTAATTCAA ATTACGAATT
B. ravenii       AAAATATCTT T--------- ---CCGATTT TGTGTAATCT AAATT----- ---------- ATTAATTAAA ATTACGAATT
B. roxburghii    AAAATATCTT T--------- ---CCGATTT TGTGTAATCT AAATT----- ---------- ATTAATTAAA ATTACGAA--
B. rubella       AAAATATCTT T--------- ---CCGATTT TGTGTAATCT AAATTTGTGT AATCTAAATT ATTAATTAAA ATTACGAATT
B. salaziensis   AAAATATCTT T--------- ---CCGATTT TGTGTAATCT CAATT----- ---------- ATTAATTCAA ATTAGGAATT
B. sutherlandii  AAAATATCTT T--------- ---CCGGTTT TGTGTAATCT CAATT----- ---------- ATTAATTCAA ATTACGAATT
B. tayabensis    AAAATATCTT T--------- ---CCGATTT TGTGTAATCT CAATT----- ---------- ATTAATTCAA ATTACGAATT
B. ulmifolia     AAAATATCTT T--------- ---CCGATTT TGTGTAATCT CCATT----- ---------- ATTAATTAAA ATTACAAATT
B. wollnyi       AAAATATTTT T--------- ---CCGATTT TGTGTAATCT CAATT----- ---------- ATTAATTCAA ATTACGAATT
Datisca          AAAATATGTT T-----?CCG GCTCC?ATTT TGTGTA?CCT CCATT----- ---------- AGTAATTGAA ATTACTAATT
Symbegonia sanguinea TAAATATCTT T--------- ---CCGATTT TGTGTAATCT CAATT----- ---------- ATTAATTCAA ATTACGAATT
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APPENDIX K CONTD.

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[                    570        580        590        600        610        620        630        640]
[                     .          .          .          .          .          .          .          .]

B. acerifolia        TGAATTTTAA AGAATCTATC TCATTCAAAT TTCACAGTGG ACTTTTGATA TATATATGTC CCATTC---- CTAATTCAA-
B. convolvulacea     TGAATTTGAA AGAATCTATC TCATTCAAAT TTCACAGTGG ACTTTTGATA TATAT--GTC CCATTC---- CTAATTCAAG
B. dipetala          TCAATTTTAA AGAATCTATC TCATTCAAAT TTCACACTGC ACTTTTGATA TATAT--GTC CCATTC---- CTAATTCAAG
B. dregei            TTAATTTTAA AGAATCTATC TCATTCAAAT TTCACACTGG GCTTTTGATA TATAT--GTC CCATTC---- CTAATTCAAG
B. floccifera        TGAATTTTAA AGAATCTATC TCATTCAAAT TTCACACTGG ACTTTTGATA TATAT--GTC CCATTC---- CTAATTCAAG
B. goegoensis        TGAGTTTTAA AGAATCTATC TCATTCAAAT TTCACACTGT ACTTTTGATA TATAT--GTC CCAGTC---- CTAATTCAAG
B. gracilis          TGAATTTTAA AGAATCTATC TCATTCAAAT TTCACACTGG ACTTTTGATA TATAT--GTC CCATTCATTC CTAATTCAAG
B. cf. grandis       TTAATTTTAA AGAATCTATC TTATTCAAAT TTCACACTGG ACTTTTGATA TATAT--GTC CCATTC---- CTAATTCAAG
B. grandis           ----TTTTAA AGAATCTATC TTATTCAAAT TTCACACTGG ACTTTTGATA TATAT--GTC CCATTC---- CTAATTCAAG
B. heracleifolia     TGAATTTTAA AGAATCTATC TCATTCAAAT TTCACACTAG ACTTTTGATA TATAT--GTC CCATTC---- CTAATTCAAG
B. incarnata         TGAATTTTAA AGAATCTATC TCATTCAAAT TTCACACTGG ACTTTTGATA TATAT--GTC CCATTC---- CTAATTCAAG
B. malachosticta     TGAATTTTAA AGAATCTATC TCATTCAAAT TTCACACTGG ACTTTTGATA TATAT--GTC CCATTC---- CTAATTCAAG
B. mannii            TTCATTTTAA AGAATCTATC TCATTCAAAT TTAACACTGG ACTTTTAATA TATAT--GTC CCATTC---- CTAATTCAAG
B. masoniana         TGAATTTTAA AGAATCTATC TCATTCAAAT TTCACACTGG ACTTTTGATA TATAT--GTC CCATTC---- CTAATTCAAG
B. maynensis         TGAATTTTAA AGAATCTATC TCATTCAAAT TTCACACTGC ACTTTTGATA TATAT--GTC CCATTC---- CTAGTTCAAG
B. meyeri johannis   TCAATTTTAA AGAATCTATC TCATTCAAAT TTCACACTGG ACTTTTGATA TATAT--GTC CCATTA---- CTAATTCAAG
B. oaxacana          ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. obliqua           TGAATTTTAA AGAATCTATC TCATTCAAAT TTCACATTGG ACTTTTGATA TATATATGTC CCATTC---- CTAATTCAAG
B. olbia             TCAATTTTAA AGAATCTATC TCATTCAAAT TTCACAGTGG ACTTTTGATA TATAT--GTC CCATTC---- CTAATTCAAG
B. aff. palmata      TTAATTTTAA AGAATCTATC TCATTCAAAT TTCACACCGG ACTTTTGATA TATAT--GTC CCATTC---- CTAATTCAAG
B. partita           TTAATTTTAA AGAATCTATC TCATTCAAAT TTCACACTGG GCTTTTGATA TATAT--GTC CCA?TC---- CTAATTCAAG
B. peltata           TTAATTTTAA AGAATCTATC TCATTCAAAT TTCACACTAG ACTTTTGATA TATAT--GTC CCATTC---- CTAATTCAAG
B. rajah             TGAGTTTTAA AGAATCTATC TCATTCAAAT TTCACACTGT ACTTTTGATA TATAT--GTC CCAGTC---- CTAATTCAAG
B. ravenii           TTAATTTTAA AGAATCTATC TCATTCAAAT TTCACACTGG ACTTTTGATA TATAT--GTC CCATTC---- CTAATTCAAG
B. roxburghii        ----TTTTAA AGAATCTATC TCATTCAAAT TTCACACTGG ACTTTTGATA TATAT--GTC CCATTC---- CTAATTCAAG
B. rubella           TTAATTTTAA AGAATCTATC TCATTCAAAT TTCACACTGG ACTTTTGATA TATAT--GTC CCATTC---- CTAATTCAAG
B. salaziensis       TGAATTTTAA AGAATCTATC TCATTCAAAT ATCACACTGC ACATTTGATA TATAT--GTC CCATTC---- CTAATTCAAG
B. sutherlandii      TGAATTTTAA AGAATCTATC TCATTCAAAT TTCACACTGC ACTTTTGATA TATAT--GTC CCATTC---- CTAATTCAAG
B. tayabensis        TGAGTTTTAA AGAATCTATC TCATTCAAAT TTCACACTGG ACTTTTGATA TATAT--GTC CCATTC---- CTAATTCAAG
B. ulmifolia         TGAATTTTAA AGAATCTATC TCATTCAAAT TTCACACTGG ACTTTTGATA TATAT--GTC CCATTC---- CTAATTCAAG
B. wollnyi           TGCATTTTAA AGAATCTATC TCATTCAAAT TTCACACTGG ACTTTTGATA TATAT--GTC CCATTC---- CTA?T?CAAG
Datisca              TGAATTTTTA ACAATCTATC TCCTTCCAAT TTCACACTGA ACTTTTTATA TATAC--GTC CCATTA---- CTAATTCAAG
Symbegonia sanguinea TGAATTTTAA AGAATCTATC TCATTCAAAT TTCACACTGG ACTTTTGATA TATAT--GTC CCATTC---- CTAATTCAAG
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APPENDIX K CONTD.

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[                    650        660        670        680        690        700        710        720]
[                BEG-TRND3-F⟶                  .          .          .          .          .]

B. acerifolia        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. convolvulacea     GAAAGA-GAT ATTACTAAGA TCAAACAAGG ATTCC-TCTC TTTTAGCGAA GGAATTTA-T ATT--ATTTT TTTAGTTTAA
B. dipetala          TAAAGAGGAT ATTACTAAGA TCAAACAAGG ATTCCATCTC TTTTAGCGAA GGAATTTTTT ATT--ATTTT TTTAGTTTAA
B. dregei            TAAAGAGGAT ATTACTAAGA TCAAACAAGG ATTCCATCTC TTTTAACGAA GTAATTTTTT ATT--ATTTT TTTAGTTTAA
B. floccifera        TAAAGAGGAT ATTACTAAGA TCAAACAAGG ATTCCATCTC TTTTAGAGAA GGAATTTTTT ATT--ATTTT TTTAGTTTAA
B. goegoensis        TAAAGAGGAT ATTACTAAGA TCAAACAAGG ATTCCATCTC TTTTAGCGAA CGCATTTTTG ATT--ATTTT GTTAGTTTAA
B. gracilis          GAAAGAGGAT ATTACTAAGA TCAAAC?AGG ATTCCATCTC TTTTAGCGAA GTAATTTTTT ATT--ATTTT TTTAGTTTAA
B. cf. grandis       TAAAGAGGAT ATTACTAAGA TCAAGCAAGG ATTCCATCTC TTTTAGCGAA GGAATTTTTT ATTTTTTTTT T-?AGTTTAA
B. grandis           TAAAGAGGAT ATTACTAAGA TCAAGCAAGG ATTCCATCTC TTTTAGCGAA GGAATTTTTT ATT--ATTTT TTTAGTTTAA
B. heracleifolia     TAAAGAAGAT ATTACTAAGA TCAAACAAGG ATTCCATCTC TTTTACCGAA GTCATTTTTT ATT--ATTTT TTTAGTTT--
B. incarnata         TAAAGAGGAT ATTACTAAGA TCAAACAAGG ATTCCATCTC TTTTAGCGAA GTAATTTTTT ATT--ATTTT TTAAGTTT--
B. malachosticta     TAAAGAGGAT ATTACTAAGA TCAAACAAAG ATTCCATCTC TTTTAGCGAA GGCATTTTTT ATY--ATTTT TTTAGTTTAA
B. mannii            TAAAGAGGAT ATTAATAAGA TCAAACAAGG ATT-CATCTC TTTTAGCGAA GGAATTTTTT ATT--ATTTT TTTAGTTTAA
B. masoniana         TAAAGAGGAT ATTACTAAGA TCAAACAAGG ATTCCATCTC TTTTAGCGAA GTAATTTTTA AT?--ATTTT TTAAGTT?AA
B. maynensis         TAAAGAGGAT ATTACTAAGA TCAAACAAGG ATTCCATCTC TTTTAGCGAA GTAATTTTTT ATT--ATTTT TTTAGTTTAA
B. meyeri johannis   TAAAGAGGAT ATTAATAAGA TCCAACAAGG ATTCCATCTC TTTTAGCGAA GGAATTTTTT ATT--CTTTT TTTA------
B. oaxacana          ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. obliqua           TAAAGAGGAT ATTACTAAGA TCAAACAAAA ATTCCATCTC TTTTAGCGAA GTCATTTTTT ATT--ATTTT TTGAGTTTAA
B. olbia             TAAAGAGGAT ATTACTAAGA TCAAACAAGG ATTCCATCGC TTTTAGCGAA GGAATTTTTT ATT--ATTTT TTTAGTTTAA
B. aff. palmata      TAAAGAGGAT ATTACTAAAA TCAAACAAGG ATTCCATCTC TTTTAGCGAA GGAATTTTTT ATT--ATTTT TTTAGTTTAA
B. partita           TAAAGAGGAT ATTACTAAGA TCAAACAAGG ATTCCATCTC TTTTAACGAA GTAATTTTTT ATT--ATTTT TTTAGTTTAA
B. peltata           TAAAGAGGAT ATTACTAAGA TCAAACAAGG ATTCCATCTC TTTTAGCGAA GTAATTTTTT ATT--ATTTT TTTAGTTT--
B. rajah             TAAAGAGGAT ATTACTAAGA TCAAACAAGG ATTCCATCTC TTTTAGCGAA GGCATTTTTG ATT--CTTTT TTTAGTTTAA
B. ravenii           TAAAGAGGAT ATTACTAAAA TCAAACAAGG ATTCCATCTC TTTTAGCGAA GGAATTTTTT ATT--ATTTT TTTAGTTTAA
B. roxburghii        TAAAGAGGAT ATTACTAAAA TCAAACAAGG ATTCCATCTC TTTTAGCGAA GGAATTTTTT ATT--ATTTT TTTAGTTTAA
B. rubella           TAAAGAGGAT ATTACTAAGA TCAAACAAGG ATTCCATCTC TTTTAGCGAA GGAATTTTTT ATT--ATTTT TTGAGTTTAA
B. salaziensis       TAAAGAGGAT ATTAATAAGA TCAAACAAGG ATTCCATCTC TTTTAGCGAA GGAATTTTTT TTT---TTTT TTTAMCTTAA
B. sutherlandii      TAAAGAGGAT ATTACTAAGA TCAAACAAGG ATTCCATCTT TTTTAGCGAA GTAATTTTTT ATT--ATTTT TTTAGTTTAA
B. tayabensis        TAAAGAGGAT ATTACTAAGA TCAAACAAGG ATTCCATCTC TTTTAGCGAA GACATTTTTT AT?--ATTTT TTTAGTTTAA
B. ulmifolia         GAAAGAGGAT ATTACTAAGA TCAAACAAGG ATTTCATCTC TTTTAGCGAA GGAATTTATT AT?--ATTTT TTTAGTTTAA
B. wollnyi           TAAAGAGGAT ATTACTAAGA TCAAACAAGG ATTCCACCTC TTTTAGAGAA GTAATTTTTT ATT--ATTTT TTTAGTTTAA
Datisca              TAAA?AGGAC ATTAATAA?A TCAAACA?GG ATCCCATC-- ------CCAG GGAATTAATT ATTTTATTTT TT-AGTTTAA
Symbegonia sanguinea TAAAGAGGAT ATTACTAAGA TCAAACAAGG ATTCCATCTC TTTTAGCGAA GGCATTTTTT ATT--ATTTT TTTAGTTTAA
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APPENDIX K CONTD.

```
[                730       740       750       760       770       780       790       800]
[                .         .         .         .         .         .         .         .]

B. acerifolia    ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. convolvulacea GT-------- --------TA AAAAAA---- ---------- ---------- ---------- ---------- ----------
B. dipetala      GT-------- --------TG AAAAAAG--- ----TTTTTT TTTTTTTTTT ---------- ---------- ----------
B. dregei        GT-------- --------TG AAAAAAG--- ----TTTCTT TCTTTT---- ---------- ---------- ----------
B. floccifera    GT-------- --------TG AAAAAAC--- ---TTTTTT TTT------- ---------- ---------- ----------
B. goegoensis    GT-------- --------TG AAAAAAG--- ----TTTTTT TTTTTT---- -AATTT---- ---------- ----------
B. gracilis      GT-------- --------TG AAAAAAG--- ----TTTTTT TTT------- --ATTA---- ---------- ----------
B. cf. grandis   GT-------- --------TG AAAAAAG--- ----T?TTTT TTTTT----- ---------- ---------- ----------
B. grandis       GT-------- --------TG AAAAAAG--- ----TATTTT TTTTT----- --A------- ---------- ----------
B. heracleifolia ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. incarnata     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. malachosticta GT-------- --------TG AAAAAAG--- ----TTTTTT TTTTTTTT-- ---------- ---------- ----------
B. mannii        GT-------- --------TG AAAAAAG--- ----TTTGTT TTTTTTTT-- --A------- ---------- ----------
B. masoniana     GT-------- --------TC AAAA------ ----TTTTTT TTTTTTTTTT T--------- ---------- ----------
B. maynensis     GT-------- --------TG AAAAAAG--- ----TTTTTT TT-------- --ATTA---- ---------- ----------
B. meyeri johannis ---------- --------G AAAAAAG--- ---------- ---------- ---------- ---------- ----------
B. oaxacana      ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. obliqua       GT-------- --------TG AAAAAAG--- ----TATTTT TTTTT----- ---------- ---------- ----------
B. olbia         GT-------- --------TA AAAAAAG--- ----TTTGTT TTTTTTTT-- --ATTAA--- ---------- ----------
B. aff. palmata  GT-------- --------TG AAAAAAG--- ----TTTTTT TT-------- --A------- ---------- ----------
B. partita       GT-------- --------TG AAAAAAG--- ----TTTCTT TCTTTT---- ---------- ---------- ----------
B. peltata       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. rajah         GT-------- --------TG AAAAAAG--- ----TTTTTT TTTTTT---- -AATTTA--- ---------- ----------
B. raveriI       GT-------- --------TG AAAAAAG--- ----TTTTTT ---------- --ATTA---- ---------- ----------
B. roxburghii    GT-------- --------TG AAAAAAG--- ----TTTTTT ---------- --ATTA---- ---------- ----------
B. rubella       GT-------- --------TG AAAAAAG--- ----TTTTTT T--------- --ATTTA--- ---------- ----------
B. salaziensis   CC-------- --------TA AAAAAAA--- ---------- ---------- ---------- ---------- ----------
B. sutherlandii  GT-------- --------TG AAAAAAC--- ----TTTTTT TTTT------ -AA------- ---------- ----------
B. tayabensis    GT-------- --------TG AAAAAAG--- ----TTTTTT TTTTTT---- ---------- ---------- ----------
B. ulmifolia     GT-------- --------TA AAAAAAG--- ----TTTGTT TTTTTTT--- --ATTAA--- ---------- ----------
B. wollnyi       GT-------- --------?G AAAAAAC--- ----TTTTTT TTTT------ ---------- ---------- ----------
Datisca          GTAAGTA?GG GTCCTGC?CG AAAAAAGAAC AAACTTATTA TTTTC----- -AATTTCGCT TCGATTGTTT GTTTGGATTG
Symbegonia sanguinea GT-------- --------TG AAAAAAG--- ----TTTTTT TTT------- --A------- ---------- ----------
```

APPENDIX K CONTD.

```
[                    810        820        830        840        850        860        870        880]
[                     .          .          .          .          .          .          .          .]

B. acerifolia        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. convolvulacea     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. dipetala          ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. dregei            ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. floccifera        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. goegoensis        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. gracilis          ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. cf. grandis       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. grandis           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. heracleifolia     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. incarnata         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. malachosticta     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. marnii            ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. masoniana         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. maynensis         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. meyeri johannis   ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. oaxacana          ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. obliqua           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. olbia             ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. aff. palmata      ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. partita           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. peltata           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. rajah             ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. ravenii           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. roxburghii        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. rubella           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. salaziensis       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. sutherlandii      ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. tayabensis        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. ulmifolia         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. wollnyi           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
Datisca              GTTTATAACC AATGTGAGTG TTTTATAACC AATGTAA?TG TAAAGCCA?T CAAAT?AT?C TTCATCAAAT GATTGT??TT
Symbegonia sanguinea ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
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APPENDIX K CONTD.

```
[                    890        900        910        920        930        940        950        960]
[                     .          .          .          .          .          .          .          .]

B. acerifolia        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. convolvulacea     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. dipetala          ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. dregei            ---------- ---------- -ATGATAAAT AAAATACTAA AAGAAACAAA TTTTTGATTG GATCAGTAAT AAAATTTAGA
B. floccifera        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. goegoensis        ---------- ---------- -ATGATAAAT AAAAT?CTAA AAAAAACAAA TTTTTGAT?G GATCAGTAAT AAAATTTATA
B. gracilis          ---------- ---------- -ATGATAAAT AAAATACTAA AAGAAACAAA TTTTTGATTG GATCATTAAT AAAATTTAGA
B. cf. grandis       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. grandis           ---------- ---------- -ATGATAAAA AAAATACTAA AAGAAACAAA TTTTTGATTG GATCAGTAAT AAAATTCAGA
B. heracleifolia     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. incarnata         ---------- ---------- ---------- ---------- ---------- ---------- ---CAGTAAT AAAATTTAGA
B. malachosticta     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. mannii            ---------- ---------- -ATGATAAAT AAAATACTAA AAGAAAGAAA TTTTGGGTTG GATCAGTAAT AAAATTTAAA
B. masoniana         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. maynensis         ---------- ---------- -ATGATAAAA AAAATACTAA AAGAAACATA TTTTTGATTG GATCAGTAAT AAAATTTATA
B. meyeri johannis   ---------- ---------T TAAAAAAAAA AAAAAAAA-- ---------- ---------- ---------- ----------
B. oaxacana          ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. obliqua           ---------- ---------- -ATCATAAAA AAAATACTAA AAGAAACAAA TTTTTGATTG GATCAGTAAT CCAATTTAGA
B. olbia             ---------- ---------- -ATGATAAAT AAAATACTAA AAGAAACAAA TTTTTGATTG GATCAGTAAT AAAATTTAAA
B. aff. palmata      ---------- ---------- -ATGATAAAT AAAATACTAA AAGAAACAAA TTTTTGATTG GATCAGTAAT AAAATTGAGA
B. partita           ---------- ---------- -ATGATAAAT AAAATACTAA AAGAAACAAA TTTTTGATTG GATCAGTAAT AAAATTTAGA
B. peltata           ---------- ---------- ---------- ---------- ---------- ---------- ---CAGTAAT AAAATTTAGA
B. rajah             ---------- ---------- -ATGATAAAT AAAATACTAA AAGAA?CAA? TTTTTGAT?G GATCACTAAT AAAATTTATA
B. ravenii           ---------- ---------- -ATGATAAAT AAAATACTAA AAGAAACAAA TTTTTGATTG GATCAGTAAT AAAATTTAGA
B. roxburghii        ---------- ---------- -ATGATAAAT AAAATACTAA AAGAAACAAA TTTTTGATTG GATCAGTAAT AAAATTTATA
B. rubella           ---------- ---------- -ATGATAAAT AAAATACTAA AAGAAACAAA TTTTTGATTG GATCAGTAAT AAAATTTAGA
B. salaziensis       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. sutherlandii      ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. tayabensis        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. ulmifolia         ---------- ---------- -ATAATAAAA AAAATACTAA AAGAAACAAA TTTGTGATTG GATCAGTAAT AAAATTTATA
B. wollnyi           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
Datisca              GTACAAGGGG GGTAGGA?GT TATAAAAAAA AAAA?AA--- ---------- ---------- ---------- ----------
Symbegonia sanguinea ---------- ---------- -ATGATAAAT AAAATACTAA AAGAAACAAA TTTTTGATTG GATCAGTAAT AAAATTTAGA
```

APPENDIX K CONTD.

```
[                    970        980        990        1000       1010       1020       1030       1040]
[                     .          .          .          .          .          .          .          .]

B. acerifolia        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. convolvulacea     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. dipetala          ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. dregei            ATTTGGTATG GATAAAAGAT CTTCCTATGT TATACTATTC AATTCTCGAC GATGAATTGA TTTGATAGTT CAAATATTGT
B. floccifera        ---------- ---GAAAGAT CTTCCTATGT TATATTATTC AATTCTCGAC GATGAATTTA TTTGATAGTT CAGATATTGT
B. goegoensis        ATT?GGT?TG GATAAAA--- ---CCTATGT TATACTATTC AATTCTCGAC AA-------- ---------- ----------
B. gracilis          AT?TGGTATG GATAAAAGAT CTTCCTATGT TATACTATTC ---------- ---------- ---------- ----------
B. cf. grandis       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. grandis           ATTTGGTATG GATAAAAGAT CTTCCTATGT TATACTATTC AATTCTCGAC GATGAATTGA TTTGATAGTT CAGATATTGT
B. heracleifolia     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. incarnata         ATTTGGTATG GATAAAAGAT CTTCCTATGT TATACTATTC AATTCTCGAC GATGAATTGA TTTGATAGTT CAGATATTGT
B. malachosticta     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. mannii            ATTTGGTATG GATAAAAGAT CT?CCTATGT TATACTAT?C AATTCTCGAC GATGAATTTA TT?GA?AGTT CAGATAT?GT
B. masoniana         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. maynensis         ATTTGGTATG GATAAAAGAT CTTCCTATGT TATACTATTC AATTCTCGAC GATGAATTGA TTTGATAGTT CAGATATTGT
B. meyeri johannis   ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. oaxacana          ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. obliqua           ATTTGATATG GATAAAAGAT CTTCCTATGT TATACTATTC AATTCTCGAC GATGAATTGA TTTGAGAGTT CAGATATTGT
B. olbia             ATTTGGTATG GATAAAAGAT CGTCCTATGT TATACTATTC AATTCTCGAC GATGAATTGA TTTAATAGTT CAAATATTGT
B. aff. palmata      ATTTGGTATG GATAAAAGAT CTTCCTATGT TATACTATTC AATTCTCGAC GATGAATTGA TTTGATAGTT CAGATATTGT
B. partita           ATTTGGTATG GATAAAAGAT CTTCCTATGT TATACTATTC AATTCTCGAC GATGAATTGA TTTGATAGTT CAAATATTGT
B. peltata           ATTTGGTATG GATAAAAGAT CTTCCTATGT TATACTATTC AATTCTCGAC GATGAATTGA TTTGATAGTT CAGATATTGT
B. rajah             ATT?GGTAGT GATAAA---- ---------- ---------- ---------- ---------- ---------- ----------
B. ravenii           ATTTGGTATG GATAAAAGAT CTTCCTATGT TATACTATTC AATTCTCGAC GATGAATTGA TTTGATAGTT C?GATATTGT
B. roxburghii        ATTTGGTATG GATAAAAGAT CTTCCTATGT TATACTATTC AATTCTCGAC GATGAATTGA TTTGATAGTT CAGATATTGT
B. rubella           ATTTGGGCTG GATAAAAGAT CTTCTTATGT TATACTATTC AATTCTCGAC GATGAATTGA TTTGATAGTT C?GATATTGT
B. salaziensis       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. sutherlandii      ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. tayabensis        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. ulmifolia         ATTTTGTATG GATAAAAGAT CTTCCCATGT TATACTATTC AATTCTCGAC GATGAATTGA TTTAATAGTT CAGATATTGT
B. wollnyi           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
Datisca              ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
Symbegonia sanguinea ATTTGATATG GATAAAAGAT CTTCCTATGT TATACTATTC AATTCTCGAC GATGAATTGA TTTGATAGTT CAGATATTGT
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APPENDIX K CONTD.

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[                    1050       1060       1070       1080       1090       1100       1110       1120]
{                     .          .          .          .          .          .          .          .]

B. acerifolia        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. convolvulacea     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. dipetala          ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. dregei            TATTCATGAT ATTCTAATAC ---------- ---------- ---------- ---------- ---------- ----------
B. floccifera        TATTCATGAT ATTCTAATAC GATTCGATAT CATCGCGATG TAATTCATAC TATTGAATTT ACAAGCCAAA GATTTATCAT
B. goegoensis        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. gracilis          ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. cf. grandis       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. grandis           TATTCATGAT ATTCTAATAC GATTCGATAT CATCGCGATG TAATTCATAC TATTGAATTT ACAAGCCAAA GATTTATCAT
B. heracleifolia     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. incarnata         TATTCATGAT ATTCTAATAC GATTCGATAT CATCGCGATG TAATTCATAC TATTGAATTT ACAAGCCAAA GATTTATCAT
B. malachosticta     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. mannii            TATTCATGAT ATTCTAATAC AATTCGATAT CACGCGA--- ---------- ---------- ---------- ----------
B. masoniana         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. maynensis         TATTCATGAT ATTCTAATAC GATTCGATAT CATCGCGATG T--------- ---------- ---------- ----------
B. meyeri johannis   ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. oaxacana          ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. obliqua           TATTCATGAT ATTCTAATAA AATTCGATAT CATCGCGATG TAATTCATA? CTATGAATTT ACAAGCCAAA GATTTATCAT
B. olbia             TATTCATGAT ATTCTAATAC GATTCGATAT C?TCGCGATG TA--------- ---------- ---------- ----------
B. aff. palmata      TATTCATGAT ATTCTAATAG GATTCGATAT CATCGCGATG TAATTCATAC TATTGAATTT ACAAGCCAAA GATTTCTCAT
B. partita           TATTCATGAT ATTCTAATAC GAA?CGATAT CATCGCGATG TAATTCATAC TATTGAATTT ACAAGCCAAA GA---------
B. peltata           TATTCATGAT ATTCTAATAC GATTCGATAT CATCGCGATG TAATTCATAC TATTGAATTT ACAAGCCAAA GATTTATCAT
B. rajah             ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. ravenii           TAT?CATGAT ATTCTAATAG ?ATTCGA--- ---------- ---------- ---------- ---------- ----------
B. roxburghii        TATTCATGAT ATTCTAATAG GATTCGATAT CATCGCGATG T?ATTCATAC TATTGAATTT ACAAGCC?AA GAATTCTCAT
B. rubella           TATTCATGAT ATTCTAATAG GATTCGATAT CATCGCGATG TAATTCATAC TATTGAATTT ACAAGCCAA- ----------
B. salaziensis       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. sutherlandii      ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. tayabensis        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. ulmifolia         TATTCATGAT AT?CTAATAC GATTCGAT?? TCACACGATG TAATTCATAC TATTGAATTT ACAAGCTAAA G---------
B. wollnyi           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
Datisca              ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
Symbegonia sanguinea TATTCATGAT ATTCTAATAC GATTCGATAT CATCGCGA?G TAATTCATAC TATTGAATTT ACAAGC---- ----------
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APPENDIX K CONTD.

```
[                    1130        1140        1150        1160        1170        1180        1190        1200]
[                     .           .           .          TRND 3'     .  TRNC 5'  .           .          3'.]

B. acerifolia        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. convolvulacea     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. dipetala          ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. dregei            ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. floccifera        TTCTATGGGA TTAAATC--- ---------- ---------- ---------- ---------- ---------- ----------
B. goegoensis        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. gracilis          ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. cf. grandis       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. grandis           TTCTATGGGA TTAAATC--- ---------- ---------- ---------- ---------- ---------- ----------
B. heracleifolia     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. incarnata         TTCTATGGGA TTAAATCCTG AGTTATTGCG AATAAAAAAA AAAAT----- ---------- ---------- ----------
B. malachosticta     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. mannii            ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. masoniana         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. maynensis         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. meyeri johannis   ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. oaxacana          ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. obliqua           TTCTATGGGA TTAAATC--- ---------- ---------- ---------- ---------- ---------- ----------
B. olbia             ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. aff. palmata      TTCTATGGGA TTAAATC--- ---------- ---------- ---------- ---------- ---------- ----------
B. partita           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. peltata           TTCTATGGGA TTAAATCC-- ---------- ---------- ---------- ---------- ---------- ----------
B. rajah             ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. ravenii           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. roxburghii        TTCTATGGGA TT?AATC--- ---------- ---------- ---------- ---------- ---------- ----------
B. rubella           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. salaziensis       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. sutherlandii      ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. tayabensis        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. ulmifolia         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. wollnyi           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
Datisca              ---------- ---------- ---------- ---------- ---------- --CCCCCCAG TCAAATCTGG GTGTCGCCTG
Symbegonia sanguinea ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
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APPENDIX K CONTD.

```
[                    1210        1220        1230        1240        1250        1260        1270        1280]
[                      .           .           .     TRNC→ .           .           .           .           .]

B. acerifolia        ---------- ---------- ---------- ---------A TATAA-CTTG C-ATTTTTTT T-ACAGAAGA AGCAAGTGGA
B. convolvulacea     ---------- ---------- ---------- ---------A TATAA-CTTG C-ATTTCTTT T-ACAGAAGA AGCAAGTGGA
B. dipetala          ---------- ---------- ---------- ---------A TATAA-CT?G ?-TTTT?TTT --CCAGCAGA AGCAAGTGGA
B. dregei            ---------- ---------- ---------- ---------A TATAA-CTTG C-ATTTTTTT --CCAGCAGA AGCAAGTGGA
B. floccifera        ---------- ---------- ---------- ---------A TATAA-CTTG C-ATTTTTTT --CCAGCAGA AGCAAGTGGA
B. goegoensis        ---------- ---------- ---------- ---------A TATAA-CTTG C-ATTTTTTT --CCAGCAGA AGCAAGTGGA
B. gracilis          ---------- ---------- ---------- ---------A TATAA-CTTG C-ATTTTTTT --CCAGCAGA AGCAAGTGGA
B. cf. grandis       ---------- ---------- ---------- ---------- ---------- ---------- --CCA?CAGA A?CAAGTGGA
B. grandis           ---------- ---------- ---------- ---------- -------TTC C-ATTTTTT- --CC?GCGG? T?CC?GTGGA
B. heracleifolia     ---------- ---------- ---------- ---------- ---------- ---------- ---------A AGCAAGTGGA
B. incarnata         ---------- ---------- ---------- ---------A TATAA-CTTG C-ATTTTTTT --CCAGCAGA AGCAAGTGGA
B. malachosticta     ---------- ---------- ---------- ---------A TATAA-CTTG C-ATTTTTTT --CCAGCAGA AGCAAGTGGA
B. mannii            ---------- ---------- ---------- ---------A TATAA-CTTG A-ATTTTT?? ---------A A?CAAGTGGA
B. masoniana         ---------- ---------- ---------- ---------A TATAA-CTTG C-ATTTTTTT --CCAGCAGA AGCAAGTGGA
B. maynensis         ---------- ---------- ---------- ---------A TATAA-CTTG C-ATTTTTTT T-CCAGCAGA AGCAAGTGGA
B. meyeri johannis   ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. oaxacana          ---------- ---------- ---------- ---------A TATAA-CTTG C-ATTTTTTT --CCAACAGA AGTT?GTGGA
B. obliqua           ---------- ---------- ---------- ---------A T?TAA-CTTG C-ATTTTTTT --CCAGCAGA AGCAAGTGGA
B. olbia             ---------- ---------- ---------- ---------A TATAA-CTTG C-ATTTTTTT --CCAGCAGA AGCAAGTGGA
B. aff. palmata      ---------- ---------- ---------- ---------A TATAA-CTTG C-ATTTTTTT T-CCAGCAGA AGCAAGTGGA
B. partita           ---------- ---------- ---------- ---------A TATAA-CTTG C-ATTTTTTT --CCAGCAGA AGCAAGTGGA
B. peltata           ---------- ---------- ---------- ---------A TATAA-CTTG C-ATTTTTTT --CCAGCAGA AGCAAGTGGA
B. rajah             ---------- ---------- ---------- ---------- ---------- ---------- ---------- ------TGGA
B. ravenii           ---------- ---------- ---------- ---------A TATAA-CTTG C-ATTTTTTT --CCA?CAGA AGCAAGTGGA
B. roxburghii        ---------- ---------- ---------- ---------A TATAA-CT?G C-ATTTCTTT --CCAGCAGA AGCAAGTGGA
B. rubella           ---------- ---------- ---------- ---------A TATAA-CT?G ?-ATTTTTTT --GCAGCAGA AGCAAGTGGA
B. salaziensis       ---------- ---------- ---------- ---------- ---------- ---------- ---------- -----GTG??
B. sutherlandii      ---------- ---------- ---------- ---------A TATAA-CTTG C-ATTTTTTT --CCAGCAGA AGCAAGTGGA
B. tayabensis        ---------- ---------- ---------- ---------A TATAA-CTTG C-ATTTTTTT TTCCAGCAGA AGCAAGTGGA
B. ulmifolia         ---------- ---------- ---------- ---------A TATAA-CT?G ?-ATTT?TTT T-CCAAAAGA AGCAAGTGGA
B. wollnyi           ---------- ---------- ---------- ---------A TATAA-CT?T C-ATTTTTTT --CCAGCAGA AGCAAGTGGA
Datisca              ATCAACAAAA GAATCGAAAT ACCCTTTTCT GTTTTGCTGA TATAAACTTG CCATTTTTTT TTCCAGCAGA AGCAA-----
Symbegonia sanguinea ---------- ---------- ---------- ---------A TATAA-CTTG C-ATTTTTTT --CCAGCAGA AGCAAGTGGA
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APPENDIX K CONTD.

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[                          1290       1300       1310       1320       1330       1340       1350       1360]
[                            .          .          .          .          .          .          .          .]

B. acerifolia              A---------- GAAAAGGACT CTTTTTATTT GCTTGATTCG AAGCATCCG- --CGTTAGGG AT-------- ----------
B. convolvulacea           A---------- GAAAAGGACT CTTTTTATTT GCTTGATTCG AAGCATCCG- --CGTTAGGG AT-------- ----------
B. dipetala                A---------- GAAAAGGACT CTTTTTATTT GCTTGATTCG AAGCATCCG- --CGTTAGGG ATTTGCTTT? CTAAAATAAA
B. dregei                  A---------- GAAAAGGACT CTTTTTATTT GCTTGATTCG AAGCATCCG- --CGTTAGGG ATTTGGTTTT CTAAAATAAA
B. floccifera              A---------- GAAAAGAACT CTTTTTATTT GCTTGATTCG AAGCATCCG- --CGTTAGGG ATTTGGTTTT CTAAAATAAA
B. goegoensis              A---------- ?AAAAGGACT CTTTTTATTT GCTTGATTCG AAGCATCCG- --CGTTAGGG ATTTGGTTTT CTAAAATAAA
B. gracilis                A---------- GAAAAGGACT CTTTTTATTT GCTTGATTCG AAGCATCCG- --CGTTAGGG ATTTGGTTTT CTAAAATAAA
B. cf. grandis             A---------- GA?A?GGA?T C?TTTTATTT GCTTGATTC? AAGCATCCG- --CGTTAAGG ATTTGGTTTT CTAAAATAAA
B. grandis                 A---------- GAAAAGGACT CTTTTTATTT GCTTGATTCG AAGCATCCG- --CGTTAGGG ATTTGGTTTT CTAAAATAAA
B. heracleifolia           A---------- GAAAAGCACT CTTTTTATTT GCTTGATTCG AAGCATCCG- --CGTTAGGG ATTTGGTTTT CTAAAATAAA
B. incarnata               A---------- GAAAAGGACT CTTTTTATTT GCTTGATTCG AAGCATCCG- --CGTTAGGG ATTTGGTTTT CTAAAATAAA
B. malachosticta           A---------- GAAAAGGACT CTTTTTATTT GCTTGATTCG AAGCATCCG- --CGTTAGGG ATTTGGTTTT CTAAAATAAA
B. mannii                  A---------- GA?AAGGGCT CTTTTTATTT GCTTGATTCG AAGTATCCG- --CATTAGGG ATTTGGTTCT CTAAAATAAA
B. masoniana               A---------- GAAAAGGACT CTTTTTATTT GCTTGATTCG AAGCATCCG- --CGTTAGGG ATTTGGTTTT CTAAAATAAA
B. maynensis               ?---------- ?AAAAGGACT CTTTT?AT?T GCTTGATTCG A?GCATCCG- --CGTTAGGG ATTTGGTTTT CTAAAATAAA
B. meyeri johannis         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. oaxacana                A---------- ?AAAAGGACT CT?TTTATTT GCTTGATTC? AAGCATCCG- --CGTTAGGG ATTTGGTTT? CTAAAATAAA
B. obliqua                 A---------- GAAAAGGACT CTTTTTATTT GCTTGATTCG AAGCATCCG- --CGTTAGGG ATTTGGTTT? CTAAAATAAA
B. olbia                   A---------- GAAAAGGACT CTTTTTATTT GCTTGATTCG AAGCATCCG- --CGTTAGGG ATTTGGTTT? CTAAAAAAAA
B. aff. palmata            A---------- GAAAAGGACT CTTTTTATTT GCTTGATTCG CAGTATCCG- --CGTTAGGG ATTTGGTTT? CTAAAATAAA
B. partita                 A---------- GAAAAGGACT CTTTTTATTT GCTTGATTCG AAGCATCCG- --CGTTAGGG ATTTGGTTT? CTAAAATAAA
B. peltata                 A---------- GAAAAGGACT CTTTTTATTT GCTTGATTCG AAGCATCCG- --CGTTAGGG ATTTGGTTT? CTAAAAAAAA
B. rajah                   A---------- CAAAAGGACT CTTTTTATTT GCTTGATTCG AA?CATCCG- --CGTTAGCG ATTTGGTTTT CTA?AATA?A
B. ravenii                 A---------- GAAAAGGACT CTTTTTATTT GCTTGATTCG CAGTATCCG- --CGTTAGGG ATTTGGTTTT CTAAAATAAA
B. roxburghii              A---------- GAAAAGGACT CTTTTTATTT GCTTGATTCG CAGTATCCG- --CGTTAGGG ATTTGGTTT? CTAAAATAAA
B. rubella                 A---------- GAAAAAGACT CTTTTTATTT GCTTGATTCG AAGTATCCA- --CGTTAGGG ATTTGGTTTT CGAAAATAAA
B. salaziensis             A---------- ?AAAAGGACT CTTTTTATTT GCTTGATTCG AAGCATCCG- --CGTTAGCA ATTTGGTTCT CTAAAATAAC
B. sutherlandii            A---------- GAAAAGGACT CTTTTTATTT GCTTGATTCG AAGCATCCG- --CGTTAGGG ATTTGGTTTT CTAAAATAAA
B. tayabensis              A---------- GAAAAGGACT CTTTTTATTT GCTTGATTCG AAGCATCCG- --CGTTAGGG ATTTT-TTTT CTAAAATAAA
B. ulmifolia               A---------- ?AAAACGACT CTTTTTATTT GCTTGATTCG AAGCATCCG- --CGTTACGG AT-------- ----------
B. wollnyi                 A---------- GAAAAGGACT CTTTTTATTT GCTTGATTCG AAGTATCCG- --CATTAGGG ATTTGGTTTT CTAAAGTAAA
Datisca                    ---------- --AAAGGACT CTTTTAATTT GCTTGATTCC AAGCATCT-- ---GTTGGGG GTTCTGTTCT CT-----AAA
Symbegonia sanguinea       AGAAGTGGAA GAAAAGGACT CTTTTTATTT GCTTGATTCG AAGCATCCG- --CGTTAGGG ATTTGGTTTT CTAAAATAAA
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APPENDIX K CONTD.

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[                    1370       1380       1390       1400       1410       1420       1430       1440]
[                     .          .          .          .          .          .      BEG-TRNC2-F→]

B. acerifolia        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. convolvulacea     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. dipetala          ATGCTATAAA TCATTGCGTC TAGGCTTCAA GGAAAGATTC TAATAATGAA ---------- ---------- ------AAGG
B. dregei            ATGCTATAAA TCATTGCGTC TAGGCTTCAA GGAAAGATTC TAATAATGAA ---------- ---------- ------AAGG
B. floccifera        ATGCTATAAA TCATTGCGTC TAGGCTTCAA GGAAAGATTC TAATAATGAA ---------- ---------- ------AAGG
B. goegoensis        ATGCTATAAA TCATTGCGTC TAGGCTTCAA GGAACGATTC TAATAATGAA TTCTAATAAT GAA------- ------AAGG
B. gracilis          ATGCTATAAA TCATTGTGTC TAGCCTTCAA GGAAAGATTC TAATAATGAA ---------- ---------- ------AAGG
B. cf. grandis       ATGCTATAAA TCATTGCGTC TAGGCTTCAA GGAAAGATTC TAAT?ATGAA ---------- ---------- ------AAGG
B. grandis           ATGCTATAAA TCGTTGCGTC TAGGCTTCAA GGAAAGATTC TAATAATGAA ---------- ---------- ------AAGG
B. heracleifolia     ATGCTATAAA TCATTGCGTC TAGGCTTCAA GGAAAGATTC TAATAATGAA ---------- ---------- ------AAGG
B. incarnata         ATGCTATAAA TCATTCCGTC TAGGCTTCAA GGAAAGATTC TAATAATGAA ---------- ---------- ------AAGG
B. malachosticta     ATGCTATAAA TCATTGCGTC TAGACTTCAA GGAAAGATTC TAATAATGAA TTCTAATAAT GAA------- ------AAGG
B. mannii            ATGCTATAAA TCATTGCGTC TAGGCTTCAA GGAAAGATTC TAATAATAAA ---------- ---------- ------AAGG
B. masoniana         ATGCTATAAA TCATTGCGCC TAGGCTTCAA GGAAAGATTC TAATAATGAA TTCTAATAAT GAA------- ------AAGG
B. maynensis         ATGCTATAAA TTATTGCGTC TCGGCTTCAA GGAAAGATTC TAATAATGAA ---------- ---------- ------AAGG
B. meyeri johannis   ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. oaxacana          ATGCT?TAAA TCATTGCGTC T?GGCTTCAA GGAAAAATTC TAATAATGAA ---------- ---------- ------AAGC
B. obliqua           ATGCTATAAA TCATTGCGTC TAGGCTTCAA GGAAAGATTC TAATAATGAA ---------- ---------- ------AAGG
B. olbia             ATGCTATAAA TCATTGCGTC TACGCTTCAA GGAAAGATTC TAATAATGAA ---------- ---------- ------AAGG
B. aff. palmata      ATGCTATAAA TCATTGCGTC TAGGCTTCAA GGAAAGATTC TAATAATGAA ---------- ---------- ------AAGG
B. partita           ATGCTATAAA TCATTGCGTC TAGGCTTCAA GGAAAGATTC TAATAATGAA ---------- ---------- ------AAGG
B. peltata           ATG------- ---TTGCGTC TAGGCTTCAA GGAAAGATTC TAATAATGAA ---------- ---------- ------AAGC
B. rajah             ATGCTAT?AA TCATTGCGTC TAGGCTTCAA GGAACGATTC T?ATAATGAA TTCTAATAAT GAA------- ------AAGG
B. ravenii           ATGCTATAAA TCATTGCGTC TAGGCTTCAA GGAAAGATTC TAATAATGAA ---------- ---------- ------AAGG
B. roxburghii        ATGCTATAAA TCATTGCGTC TAGGCTTCAA GGAAAGATTC TAATAATGAA ---------- ---------- ------AAGG
B. rubella           ATGCTATAAA TCATTGCGTC TAGGCTTCAA GGAAAGATTC TAATAATGAA ---------- ---------- ------AAGG
B. salaziensis       ATGCTATAAA TCATTGCGTC TAGGCTTCAA GGAAAGATTC TAATAATGAA ---------- ---------- ------AAGG
B. sutherlandii      ATGCTATAAA TCATTGCGTC TAGGCTTCAA GGAAAGATTC TAATAATGAA ---------- ---------- ------AAGG
B. tayabensis        ATGCTATAAA TCATTGCGTC TAGGCTTCAA GGAAAGATTC TAATAATGAA TTCTAATAAT GAA------- ------AAGG
B. ulmifolia         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. wollnyi           ATGCTATAAA TTATTGCGTC TAGGCTTCAA GGAAAGATTC TAATAATGAA ---------- ---------- ------AAGC
Datisca              ATGCTATCAA TCCTTGCGTC TAGGCTTCAA GGAAAGATTA TAGTAGTGAA ---------- ---------- ------AAAG
Symbegonia sanguinea ATGCTATAAA TCATTGCGTC TAGGCTTCAA GGAAAGATTC TAATAATGAA TTCGAATAAT GAA------- ------AAGC
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APPENDIX K CONTD.

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[                                    1450        1460        1470        1480        1490        1500        1510        1520]
[                BEG-TRNC2-F------------------------>.           .           .           .           .           .           .]

B. acerifolia          ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. convolvulacea       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. dipetala            AATCATTAAA TCTTGATATG ATAGTCTTTT GACTACTAAT ---------- ---------- ---------- ----------
B. dregei              AATCATTAAA TCTTGATATG ATAGTCTTTT GACTACTAAT ---------- ---------- ---------- ----------
B. floccifera          AATCATTAAA TCTTGATATG AGAGTCTTTT GACTACTAAT CTAAT----- ---------- ---------- ----------
B. goegoensis          AATCATTAAA TCTTGATATG ATAGTCTTTT GACTACTAAT ---------- ---------- ---------- ----------
B. gracilis            AATCATTAAA TCTTGATATG ATAGTCTTTT GACTACTAAT ---------- ---------- --------AT AGAATTATCA
B. cf. grandis         AATCATTAAA TCTTGATATG ATA?TCTTTT GACTACTAAT ---------- ---------- ---------- ----------
B. grandis             AATCATTAAA TCTTGATATG ATAGTCTTTT GACTACTAAT -----ATGAT AGTCTTTTGA CTACTAAT-- ----------
B. heracleifolia       AATCATTAAA TCTTGATATG ATAGTCTTTT GACTACTAAT ---------- ---------- --------AT AGAATTATCA
B. incarnata           AATCATTAAA TCTTGATATG ATAGTCTTTT GACTACTAAT ---------- ---------- --------AT AGAATTATCA
B. malachosticta       AATCATTAAA TCTTGATATG ATAGTCTTTT GACTACTAAT ---------- ---------- ---------- ----------
B. mannii              AATCATTAAA TCTTGATATG GTAGTCGAAA GACTACTAAT ---------- ---------- ---------- ----------
B. masoniana           AATCATTAAA TCTTGATATG ATAGTCTTTT GACTACTAAT ---------- ---------- ---------- ----------
B. maynensis           AATCATTAAA TCTTGATATG ATAGTCTTTT GACTACTGAT ---------- ---------- --------AT AGAATCATCA
B. meyeri johannis     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. oaxacana            AATCATTAAA TCTTGATATG ATAGTCTTTT AACTACTAAT ---------- ---------- --------AT AGAATTATCA
B. obliqua             AATCATTAAA TCTTGATATG ATAGTCTTTT GACTACTAAT ---------- ---------- --------AT AGAATTATCA
B. olbia               AATCATTAAA ACTTGATATG ATAGTCTTTT GACTACTAAT ---------- ---------- ---------- ----------
B. aff. palmata        AATCATTAAC TCTTGATATG ATAGTCTTTT GACTACTAAT ---------- ---------- ---------- ----------
B. partita             AATCATTAAA TCTTGATATG ATAGTCTTTT GACTACTAAT ---------- ---------- ---------- ----------
B. peltata             AATCATTAAA TCTTGATATG ATAGTCTTTT GACTACTAAT ---------- ---------- --------AT AGAATTATCA
B. rajah               AATCATTAAA TCTTGATATG ATAGTCTTTT GACTACTAAT ---------- ---------- ---------- ----------
B. ravenii             AATCATTAAA TCTTGATATG ATAGTCTTTT GACTACTAAT ---------- ---------- ---------- ----------
B. roxburghii          AATCATTAAA TCTTGATATG ATAGTCTTTT GACTACTAAT ---------- ---------- ---------- ----------
B. rubella             AATCATTAAA TCTTGATATG ATAGTCTTTT GACTACTAAT ---------- ---------- ---------- ----------
B. salaziensis         AATCA----- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. sutherlandii        AATCATTAAA TCTTGATATG ATAGTCTTTT GACTACTAAT ---------- ---------- --------AT AGAATTATCA
B. tayabensis          AATCATTAAA TCTTGATATG ATAGTCTTTT GACTACTAAT ---------- ---------- ---------- ----------
B. ulmifolia           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. wollnyi             AATCATTAAA TCTTGATATG ATAGTCTTTT GACTACTGAT ---------- ---------- --------AT AGAATTATCA
Datisca                AATCATTAAA TCTTGATATG ATAGCCCTTC GACTACTAAT ---------- ---------- ---------- ----------
Symbegonia sanguinea   AATCATTAAA TCTTGATATG ATAGTCTTTT GACTACTAAT ---------- ---------- ---------- ----------
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APPENDIX K CONTD.

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[                    1530        1540        1550        1560        1570        1580        1590        1600]
[                     .           .           .      <-------------BEG-TRNC1-R     .                       ]

B. acerifolia        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. convolvulacea     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. dipetala          ---------- ---------- ---------- ------GTAG TGGCTGCTGA CTGGTTCTTA AATGAGATT- -GGATATATG
B. dregei            ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. floccifera        ---------- ---------- ---------- ------GTAG TGGCTGCTGA CTGGTTCTTA AATGAGATT- -GGATATATG
B. goegoensis        ---------- ---------- ---------- ------GTAG TGGCTGCTAA CTGGTTCTTA AATGAGATT- -GGATATATG
B. gracilis          ATAGAATTAT CTATTGAATA GATAATTCTA TTTTTC---- ---------- ---------- ---------- ----------
B. cf. grandis       ---------- ---------- ---------- ------GTAA TGGCTGCTGA CTGGTTCTAA AATGAGATT- -GGATATATG
B. grandis           ---------- ---------- ---------- ------GTAG TGGCTGCTGA CTGGTTCTAA AATGAGATT- -GGATATATG
B. heracleifolia     ATAGAATTAT CTATTCAATA GATAATTTTT TTT------- ---------- ---------- ---------- ----------
B. incarnata         ATAGAATTAT CTATTGAATA GATAATTTTT TTTT------ ---------- ---------- ---------- ----------
B. malachosticta     ---------- ---------- ---------- ------GTAG TGGCTGCTAA CTGGTTCTTA AATGAGATT- -GGATATATG
B. mannii            ---------- ---------- ---------- ------GGAG TGGCTGCTGG CTGGTTCTTA AATGAGATT- -GGATATACA
B. masoniana         ---------- ---------- ---------- ------GTAG TGGCTGCTAA CTGGTTCTTA AATGAGATT- -GGATATATG
B. maynensis         ATAGAATTAT CTATTGAATA GATAAT?TTT TTTTT----- ---------- ---------- ---------- ----------
B. meyeri johannis   ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. oaxacana          ATAGAATTAT CTATTGAATA GATAATTTTA TTTT-C---- ---------- ---------- ---------- ----------
B. obliqua           ATAGAATTAT CTATTGAATA GATAATTTTT TTTT-C---- ---------- ---------- ---------- ----------
B. olbia             ---------- ---------- ---------- ------GTAG TGGCTGCTGC CTGGTTCTTA AATGAGGTG- -GGATATGTG
B. aff. palmata      ---------- ---------- ---------- ------GTAG TGACTGCTGA CTGGTTCTAA AATTAGATT- -GGATATATG
B. partita           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. peltata           ATAGAATTAT CTATTGAATA GATAATTTTA TTTT-C---- ---------- ---------- ---------- ----------
B. rajah             ---------- ---------- ---------- ------GTAG TGGCTGCTAA CTGGTTCTTA AATGAGATT- -GGATATATG
B. ravenii           ---------- ---------- ---------- ------GTA? TGACTGCTGA CTGGTTCTAA AATGAGATT- -GGATATATG
B. roxburghii        ---------- ---------- ---------- ------GTAG TGACTGCTGA CTGGTTCTAA AATGAGATT- -GGATATATG
B. rubella           ---------- ---------- ---------- ------GTAA TGACTGCTGA CTGGTTCTAA AATGAGATT- -GGATATATG
B. salaziensis       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. sutherlandii      ATAGAATTAT CTACTGAATA GATAATTTTT TTTTTT---- ---------- ---------- ---------- ----------
B. tayabensis        ---------- ---------- ---------- ------CTAG TGGCTGCTAA CTGGTTCTTA AATGAGATT- -GGATATATG
B. ulmifolia         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. wollnyi           ATAGAATTAT CTATTGAATA GATAATTTTT TTTT------ ---------- ---------- ---------- ----------
Datisca              ---------- ---------- ---------- ------GTAG TGGCTACTGA CTGGGTCTTG AATTAGATTT TGTATAGACG
Symbegonia sanguinea ---------- ---------- ---------- ------GTAG TGGCTGCTAA CTGGTTCTTA AATGAGATT- -GGATATATG
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APPENDIX K CONTD.

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[                    1610        1620        1630        1640        1650        1660        1670        1680]
[                     .           .          <---------- DAT-TRNC-3    .           .           .          .]

B. acerifolia        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. convolvulacea     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. dipetala          TATACCCGAT CTATT----- --TTAGTTTC GGAAA--GCG GAAGATACTT TATGTAC--- -TTATGAAAA T----------
B. dregei            ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. floccifera        TATAGGGGAT CTATT----- --TTATTTTC GGAAA--GCG GAAGATACTT TATGTAC--- -TTATGAAAA T----------
B. goegoensis        TATAGGGGAT CTATT----- --TTAGTTTC GGAAA--GCG GAAGATACTT TATGTAC--- -TTATGAAAA T----------
B. gracilis          ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. cf. grandis       TATAGGGGAT CTATT----- --TTAGTTTC GGAAA--GCG GAAGATACTT TATGTAC--- -TTATGAAAA T----------
B. grandis           TATAGGGGAT CTATT----- --TGAGTTTC GGAAA--GCG GAAGATACTT TATGTAC--- -TTATGAAAA T----------
B. heracleifolia     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. incarnata         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. malachosticta     TATAGGGGAT CTATT----- --TTAGTTTC GGAAA--GTG GAAGATACTT TATGTAC--- -TTATGAAAA TATGTACTTA
B. mannii            TCC?GGAGAT CTTTT----- --TTAGTTGC GGAAA--GCG GAAGATACTT TATGTAC--- -TTATGAAAA T----------
B. masoniana         TATAGGGGAT CTATT----- --TTAGTTTC GGAAA--GCG GAAGATATTT TATGTAC--- -TTATGAAAA T----------
B. maynensis         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. meyeri johannis   ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. oaxacana          ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. obliqua           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. olbia             TATAGGGGAT CC-TT----- --TTAGTTTC GGAA------ ---------- ---------- ---------- ----------
B. aff. palmata      TATAGGGGAT CTATT----- --TTAGTTTC GGAAA--GCG GAAGATACTT TATATAC--- -TTATGAAAA G----------
B. partita           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. peltata           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. rajah             TATAGGGGAT CTATT----- --TGAGTTTC GGAAA--GCG GAAGATACTT TATGTAC--- -TTATGAAAA T----------
B. ravenii           TATAGGGGAT CTATT----- --TTAGTTTC GGAAA--GCG GAAGATACTT TATATAC--- -TTATGAAAA T----------
B. roxburghii        TATAGGGGAT CTATT----- --TTAGTTTC GGAAA--GCG GAAGATACTT TATATAC--- -TTATGAAAA T----------
B. rubella           TATAGGGGGT CTATT----- --TTAGTTTC GGAAA--GTG GAAGATACTT TATGTAT--- -TTATGAAAA T----------
B. salaziensis       ---------- ---------- ---------- ---------- ---------T TATGTAC--- -TTATGAAAA ?----------
B. sutherlandii      ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. tayabensis        G--------T CTATT----- --TTAGTTTC GGAAA--GCG GAAGATACTT TATGTAC--- -TTATGAAAA ----------
B. ulmifolia         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. wollnyi           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
Datisca              TATAGGGAAT C?AATGAAAT TCTTAGTTAC AGAAAGGGCG CAAGATACTT TATATACGGA CTCATGAAAG T----------
Symbegonia sanguinea TATAGGGGAT CTATT----- --TTAGTTTC GGAAA--GCG GAAGATACTT TATGTAC--- -TTATGAAAA T----------
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APPENDIX K CONTD.

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[                1690       1700       1710       1720       1730       1740       1750       1760]
[                   .          .          .          .          .          .          .          .]

B. acerifolia    ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. convolvulacea ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. dipetala      -------AAA ATCTCTGATT GTTCCCGGAT TCAATTATTA T-----TCTA TTCAA----- TAGAATTATC TATTGAATAG
B. dregei        ---------- ---------- ---------- ---------- ---------- ----A----- TAGAATTATC ----------
B. floccifera    -------AAA ATCTCTGATT GTTCCCGGAT TCAATTATTA T-----TCTA TTCAA----- ATTATTATTC TATTCAATAG
B. goegoensis    -------AAA ATCTCTGATT GTTCCCGTAT TCAATTATTA T-----TCTA TTCAA----- TAGAATTATC TATTGAATAA
B. gracilis      ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. cf. grandis   -------CAA ATCTCTGATT GTTCCCGGAT TCAATTATTA T-----TCTA TTCAA----- TAGAATTATC TATTCAATAG
B. grandis       -------CAA ATCTCTGATT GTTCCCGGAT TCAATTATTA T-----TCTA TTCAA----- TAGAATTATC TATTCAATAG
B. heracleifolia ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. incarnata     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. malachosticta TGAAAATAAA ATCTCTGATT GTTCCCGGAT TCAATTATTA T-----TCTA TTCAA----- TAGAATTATC TATTGAATAG
B. mannii        -------AAA ATCTCTGATT GTTCCCGCAT TCAATTATAA T-----TCTA TTCAA----- TAGAATTATC TATTGAATAG
B. masoniana     -------AAA ATCTCTGATT GTTCCCGGAT TCAATTATTA T-----TCTA TTCAA----- TAGAATTATC TATTGAATAG
B. maynensis     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. meyeri johannis ---------A ATCTCTGATT GTTCCCGCA? TCAATTATTA GTCTATTCGA TACA?----- TTAGCTACTG A?CACA----
B. oaxacana      ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. obliqua       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. olbia         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. aff. palmata  -------AAA ATCTCTGATT GTTCCCGGAT TCAATTATTA T-----TCTA TTTT------ ---------- ----------
B. partita       ---------- ---------- ---------- ---------- ---------- ----A----- TAGAATTATC -----AATAG
B. peltata       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. rajah         -------AAA ATCTCTGATT GTTCCCGGAT TCAATTATTA T-----TCTA TTCAA----- TAGAATTATC TATTGAATAA
B. ravenii       -------AAA ATCTCTGATT GTTCCCGGAT TCAATTATTA T-----TCTA TTCAA----- TAGAATTATC TATTGAATAG
B. roxburghii    -------AAA ATCTCTGATT GTTCCCGGAT TCAATTATTA T-----TCTA TTTT------ ---------- ----------
B. rubella       -------AAA ATCTCTGATT GTTCCCGGAT TCAATTATTA T-----TCTA TTCAATTCAA TAGAATTATC TATTCAATAG
B. salaziensis   -------AAA ATCTCTGATT GTTCCCGCAT TCAATTATTA TATTATTCTA TTCAA----- TAGAATTATC TATTCAATAG
B. sutherlandii  ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. tayabensis    -------AAA ATCTCTGATT GTTCCCGGAT TCAATTATTA T-----TCTA TTCAA----- TAGAATTATC TATTGAATAG
B. ulmifolia     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. wollnyi       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
Datisca          ---------- --TTCTGAGT GCTCCAGCAT T---TTAT-- ---------- ---------- --CACTATTA TATTGAATGG
Symbegonia sanguinea -------AAA ATCTCTGATT GTTCCCGGAT TCAATTATAA T-----TCTA TTCAA----- TAGATAATTC TATTGAATAG
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APPENDIX K CONTD.

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[                1770       1780       1790       1800       1810       1820       1830       1840]
[                   .          .          .          .          .          .          .          .]

B. acerifolia    ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. convolvulacea ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. dipetala      A--------- --------TA ATTTTTTTTT --GTTCTATA ACTTTTTA-- --GAAAGTTA TATT------ --------AA
B. dregei        -------TAT TGAATAGATA ATTTTTTTTT T--------- ---------- ---------- ---------- ----------
B. floccifera    AATTATCTAT TGAATAGATA ATTTTTTTTT ?-GT?CTATA ACTTTTTATT TTAAAAGTTA TATT------ ----------AA
B. goegoensis    A--------- --------TA ATTTTTTTTT TTG------- ---------- ---------- ---------- ----------
B. gracilis      ---------- ---------- ---------- --GTTCTATA ACTTTTTA-- --GAAAGTTA TATT------ --------AA
B. cf. grandis   A--------- --------TA ATTTTTTTT- --GTTCTATA ACTTTTTA-- --GAAAGTTA TATT------ --------AA
B. grandis       A--------- --------TA ATTTTTTTT- --GTTCTATA ACTTTTTA-- --GAAAGTTA TATT------ --------AA
B. heracleifolia ---------- ---------- ---------- --GTTCTAT? ACTTTCTA-- --GAAAGTTA TATT------ --------AA
B. incarnata     ---------- ---------- ---------- --GTTCTATA ACTTTTTA-- --GAAAGTTA TATT------ --------AA
B. malachosticta A--------- --------TA ATTTTTTTTT --GTTCTATA ACTTTTTA-- --GAAAGTTA TATT------ --------AA
B. mannii        A--------- --------TA ATTTTGTTTT C-GTTCTATA ACTTTTTA-- --GAAAATTT TAATATT--- --------AA
B. masoniana     A--------- --------TA ATTTTTTTTT --GTTCTATA ACTTTTTA-- --GAAAGTTA TATT------ --------AA
B. maynensis     ---------- ---------- ---------- --GTTCTATA ACTTTTTA-- --GAAAATTA TATT------ --------AA
B. meyeri johannis ---------- --------TA ATTTAGTTTT C-GTGCTATA ?CTTTTTA-- --GAAAGTTA ?AT?A----- ---------A
B. oaxacana      ---------- ---------- ---------- --GTTCTATA ACTTTTTA-- --AAAAGTTA TATT------ --------AA
B. obliqua       ---------- ---------- ---------- --GTTCTATA ACTTTTTA-- --GAAAGTTA TATT------ --------AA
B. olbia         ---------- --AATAGATA ATTTTGTTTT C-GTTCTATA ACTTTTTA-- --GAAAGTTA TATT------ --------AA
B. aff. palmata  ---------- ---------- ---------- --GTTCTATA ACTTTTTA-- --GAAAGTTA TATT------ --------AA
B. partita       AATTATCTAT TGAATAGATA ATTTTTTTTT T--------- ---------- ---------- ---------- ----------
B. peltata       ---------- ---------- ---------- --GTTCTATA ACTTTTTA-- --GAAAGTTA TATT------ --------AA
B. rajah         A--------- --------TA ATTTTTTTTT T--------- ---------- ---------- ---------- ----------
B. ravenii       A--------- --------TA ATTCTATTTT --GTTCTATA ACTTTTTA-- --GAAAGTTA TATT------ --------AA
B. roxburghii    ---------- ---------- ---------- --GTTCTATA ACTTTTTA-- --GAAAGTTA TATT------ --------AA
B. rubella       A--------- --------TA ATTCTATTTT --GTTCTATA ACTTTTTA-- --GAAAGTTA TATT------ --------AA
B. salaziensis   A--------- --------TA ATTTTGTTTT C-GTTCTATA ACTTTTTA-- --GAAAGTTA TATT------ --------AA
B. sutherlandii  ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. tayabensis    A--------- --------TA ATTTTTTTT? --GTTCTATA ACTTTTTA-- --GAAAGTTA TATT------ --------AA
B. ulmifolia     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. wollnyi       ---------- ---------- ---------- --GTTCTATA ACTTTTTA-- --GAAAGTTA TATT------ --------AA
Datisca          A--------- --------T? ?TTGGCTTTT A-CTTATATA ACTTTCTA-- --GAAAGTTA TATT---ATA TTAAGTTTAA
Symbegonia sanguinea A--------- --------TA ATTTTTTTTT --GTTCTATA ACTTTTGA-- --GAAAGTTA TATT------ --------AA
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APPENDIX K CONTD.

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[                    1850       1860       1870       1880       1890       1900       1910       1920]
[                     .          .          .          .          .          .          .          .]

B. acerifolia        --------AA AGCGAATTCC TTCTTTTTGG TAACCCACAG TCAC?AATGT ?ATAGGCCGT CTACCAAGCG ACTCTATGAA
B. convolvulacea     --------AA AGCGAATTCC TTCTTTCTGG TAACCCACAG TCACGAATGT AATAGGCCGG CTACCAAGCG ACTCTATGAA
B. dipetala          GT---AAAAA AGCGAATTCC TTCTTTTTGG TAACCCGCAG TCACGAATGG AATAGGCCGT CTCCCGAGCG ACTCTATGAA
B. dregei            ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. floccifera        GT---AAAAA AGCGAATTCC TTCTTTT?GG TAACCCGCAG TCAC?AATGG AATAGGCCGT CTCCCGAGCG ACTCTATGAA
B. gocgoensis        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. gracilis          GA---AAAAA AGCGAATTCC TTCTTTTTGG TAACCCGCAG TCGCGAATGG AATAGGCCGT TTCTCGAGCG ACTCTATGAA
B. cf. grandis       GT---AAAAA AGCGAATTCC TTCTTTTTGC TAACCCGCAG TC?C?AATGG AATAGGCCGT CTCCC?AGCG ACTCTATGAA
B. grandis           GT---AAAAA AGCGAATTCC TTCTTTTTGG TAACCCGCAG TCACGAATGG AATAGGCCGT CTCCCGAGCG ACTCTATGAA
B. heracleifolia     GT---AAAAA AGCGAATTCC TTCTTTTTGG TAACCCGCAG TCACGAATGG AATAGGCCGT TTCTCGAGCG ACTCTATGAA
B. incarnata         GT---AAAAA AGCGAAT?CC TT-------- ---------- ---------- ---------- ---------- ----------
B. malachosticta     GT---AAAAA AGCGAATTCC TTCTTTTTGG TAACCCGCCG TCACGAATGG AATAGGCCGT CTCCCGAGCG ACTCTATGAA
B. mannii            GT---AAAAA AGCAAATTTA TTATTTTTGG TAACCCGTAC TCAC?AATGG AATAGGCCGT CTCCCAAGCT ACTCTATGAA
B. masoniana         GT---AAAAA AGAGAATTCC ?TCTTTTTGG T?ACCCGCAG TC?CCAATGG AATAGGCCGT CTCCCGAGCG ACTCTTTGA?
B. maynensis         GT---AAAAA AGCGAATTCC TTCTTTTTGG TAACTCGCAG T--CGAATGG AATAGGCCGT TTCTCAAGCG ACTCT-TGAA
B. meyeri johannis   GT---??AAA AGCGAATTTC TTCTTTTTGG TAACCCGTAC TCA??AATGG AA?AAGCCAT CTCCCGAGCG ACTCTATGAA
B. oaxacana          GT---AAAAA AGCGAATTCC TTCTTTTTGG TAACCCGCAG TCACGAATGG AATAGGCCGT TTCTCCACCA ACTCTATGAA
B. obliqua           GT---AAAAA AGCGAATTCC TTCTTTTTGG TAACCCGCAG TCACGAATGG AATAGGCCGT TTCTCGAGCG ACTCTATGAA
B. olbia             GT---AAAAA AGCGAATTCC TTCTTTTTGG TAACCCACAG TCACGAATGG AATAGGCCGT CTCCCAAGCG ACTCTATGAA
B. aff. palmata      GT---AAAAA AGCGAATTCC TTCTTTTTGG TAACCCGCAG TCACGAATGG AATAAGCCGT CTCCCGAGCG ACTCTATGAA
B. partita           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. peltata           GT---AAAAA AGCGAATTCC TTCTTTTTGG TAACCCGCAG TCACGAATGG AATAGGCCGT TTCTCGAGCG ACTCTATGAA
B. rajah             ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. ravenii           GT---AAAAA AGCGAATTCC TTCTTTTTGG TAACCCGCAG TCACGAATGG AATAGGCCGT CTCCCGAGCG ACTCTATGAA
B. roxburghii        GT---AAAAA AGCGAATTCC TTCTTTTTGG TAACCCGCAG TCACGAATGG AATAGGCCGT CTCCCGAGCG ACTCTATGAA
B. rubella           GT---AAAAA AGCGAATTCC TTCTTTTTGG TAACCCGCAG TCACGAATGG AATACGCCGT CTCCCGAGCG ACTCTATGAA
B. salaziensis       GT---AAAAA AGCGAATTCC TTCTTTTTGG TAACCTGTAG TCACGAATGG AATAGGCCGT CTCCCGAGCG ACTCTATGAA
B. sutherlandii      ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. tayabensis        GT---AAAAA AGCGAATTCC TTCTTTT?GG TAACCCACAG TCACAAATGG AATAGGTCGT CTCCCAAGTC ACTCTATGAA
B. ulmifolia         --------AA AGCGAATTCC TTCTTTTTGG TAACCCACAG TCACGAATGT AATAGGCCGT CTACCAAGCG ACTCTATGAA
B. wollnyi           GT---AAAAA AGCGAATTCC TTCTTTTTGG TAACCCGCAG TTACGAATGG AATAGGCCGT TTCTCGAGCG ACTCTATGAA
Datisca              GTCAAAAAAA AAGGAATTC- ---TTTT?GG TAACCCCTA? TCACGAACGG AATAGGCCGT CCCCCGATTC TTTCATAAAG
Symbegonia sanguinea GT---AAAAA AGCGAATTCC TTCTTTTTGG TAACCCGCAG TCACGAATGG AATAGGCCGT CTCCCGAGCG ACTCTATGAA
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APPENDIX K CONTD.

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[                          1930        1940        1950        1960        1970        1980        1990        2000]
[                             .           .           .           .           .           .           .           .]

B. acerifolia              ACAA-----T T-GATAGACG GTAAAGATTA GACCAAATGA CAAAGGAGTA -GGTATG-TG --------TG ATCTAACTTG
B. convolvulacea           ACAA-----T T-GATAGACG GTAAAGATTA GACCAAATGA CAAAGGAGTA -GGTATG-TG --------TG ATCTAACTTG
B. dipetala                ACAA-----T T-AGGAGACG GTAAAGATTA GATCAAATGA GAAAGGAGTA -GGTATG-TG --------TG ATCTAGCTTG
B. dregei                  ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. floccifera              ACAA-----T T-AGGAGACG GT?AAAATTA ?ATCAAATGA GAAAGGAGTA -GGTATG-TG --------TG ATCTACCTTG
B. gocgoensis              ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. gracilis                ACAA-----T T-AGGAGACG GTAAAGATTA GATCAAATGA GAAAGGAATA -GGTATG-TG --------TG ATCTA?CTTA
B. cf. grandis             ACAA-----T T-AGGAGACG GTAAAGATTA ?ATCA?ATGA CAAAGGAGTA -GGTATG-TG --------TG ATCTACCTTG
B. grandis                 ACAA-----T T-AGGAGACG GTAAAGATTA GATCAAATGA GAAAGGAGTA -GGTATG-TG --------TC ATCTAGCTTG
B. heracleifolia           ACAA-----T T-AGGAGACG GTAAAGATTA GATCAAATGA GAAAGGAATA -GGTATG-TG --------TG ATCTAGCTTG
B. incarnata               ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. malachosticta           ACAA-----T T-AGGAGACG GTAAAGATTA ?ATCAAATGA GAAAGGAGTA -GGTATG-TG --------TG ATCTAGCTTG
B. mannii                  ACAG-----T T-GGGAGACG GTCAAGATTA ?ATCAAATGA GAAAGGAGTA -GGTATG-TG --------TG ATCTAGCTTG
B. masoniana               ACAA-----T T-?GGA?ACG GT?AAGATTA ?ATCAAATGA ?AAAGGA?TA -GGTATG-TG --------TG ATCTACCTTG
B. maynensis               ACGAACCA?T T-AGGAGACG GTAAAGATTA GATCAAATGA CAAAGGAGTA -GGTATG-TG --------TG A?CTAGCTTG
B. meyeri johannis         ACAA-----T ?-GGGAGACG GTAA?GATTA GATCA?ATGA GAGAGGAGTA -CGTATG-TG --------TG ATCTA?CTTG
B. oaxacana                ACAA-----T T-AGGAGACG GTAAAGATTA GATCAAATGA GAAAGGAATA -GGTATG-TG --------TG ATCTACCTTG
B. obliqua                 ACAA-----T T-AGGAGACG GTAAAGATTA GATCAAATGA GAAAGGAATA -GGTATG-TG --------TG ATCTAGCTTG
B. olbia                   ACAA-----T T-CGGAGACG GTAAAGATTA GACCAAATGA GAAAGGAGTA -GGTATG-TG --------TG ATCTAACTTG
B. aff. palmata            ACAA-----T T-AGGAGACG GT?AAGATTA GATCAAATGA GAAAGGAATA -?GTATG-TG --------TG ATCTAGCTCG
B. partita                 ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. peltata                 ACAA-----T T-AGGAGACG GTAAAGATTA GATCAAATGA GAAAGGAATA -GGTATG-TG --------TG ATCTACCTTG
B. rajah                   ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. ravenii                 ACAA-----T T-ACGAGACG GTAAAGATTA GATCAAATGA GAAAGGAATA -GGTATG-TG --------TG ATCTAGCTTG
B. roxburghii              ACAA-----T T-AGGAGACG GTAAAGATTA GATCAAATGA GAAAGGAATA -GGTATG-TG --------TG ATCTAGCTTG
B. rubella                 ACAA-----T T-AGGAGACG GTAAAGATTA GATCAAATGA GAAAGGAATA -GGTATG-TG --------TG ATCTAGCTTG
B. salaziensis             ACAA-----T T-GGGAGACG GT?AAGATTA GATCAAATGA GAAAGGAATA -GGTATG-TG --------TG ATCTAGCTTG
B. sutherlandii            ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. tayabensis              ACAA-----T T-AGGAGACG GTAAAGATTA GATCACATGA GAAAGGAGTA -GGTATG-TG --------TG ATCTACCTTG
B. ulmifolia               ACAA-----T T-GATAGACG GTAAAGATTA GACCAAATGA CAAAGGAGTA -GGTATG-TG --------TG ATCTAACTTG
B. wollnyi                 ACAA-----T T-AGTACACG GTAAAGATTA GATCAAATGA GAAAGGA?TA -GGTATG-TG --------TG A?CTA?CTTG
Datisca                    ACAA-----T CCGGGAGACG GTAAAAATTA AATCAAATGA GAAAGGAATA ?GGAAGGGTG ATAAATAATG ATCTATCTTG
Symbegonia sanguinea       ACAA-----T T-AGGAGACG GTAAAGATTA GATCAAATGA GAAAGGAGTA -GGTATG-TG --------TC ATCTAGCTTG
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APPENDIX K CONTD.

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[                2010       2020       2030       2040       2050       2060       2070       2080]
[                .          .          .          .          .          .          .          .]

B. acerifolia    ATTCTCAACT T--------- -----AAAAA AAAAATGAAA TGGAGGGCAA CAAAA?AAAG GCAAAGTTTT TCCATTAGAC
B. convolvulacea ATTCTCAACT T--------- ------AAAA AAAAATGAAA TGGAGGGCAA CAAAAGAAAG GCAAACTTTT TCCATTA?AC
B. dipetala      ATTCTCAACT TTTCT--ACT TTTT-----A AAAAATGAAA TGGAGGGCAA C?AAAGAAAG ACAAAGTTTT TCCATTAGAC
B. dregei        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. floccifera    ATTCTCAACT TT?CT--ACT TTTT-----A AAAA?TGAAA TGGAGGGC?? CAAAAAAAAA ACAAAGTTTT TCCATTAGAC
B. goegoensis    ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. gracilis      ATTCTCAACT TTTCT--ACT TTTT-----C AAAAATGAAA TGTAGGGCAA CAAAAGAAAG ACAAAGTTTT TCCATTAGAC
B. cf. grandis   ATTCTCAACT TTTCT--ACT TTT-----GA AAAAATGAAA TGGAGGGCAA CAAAAGAAAG ACCAAGTTTT TCCATTAGAC
B. grandis       ATTCTCAACT TTTCT--ACT TTT-----GA AAAAATGAAA TGGAGGGCAA CAAAAGAAAG ACCGAGTTTT TCCATTAGAC
B. heracleifolia ATTCTCAACT TTTCT--ACT TTTT-----C AAAAATGAAA TGGAGGGCAA CAAAAGAAAG ACAAAGTTTT TCCATTAGAC
B. incarnata     ---------- ---------- ---------- ---------- ---------- ---------- -----GTTTT ?CCATTAGAC
B. malachosticta ATTCTCAACT TTTCT--ACT TTTT-----A AAAAATGAAA TGGAGGGCA? CAAAAAAAAG ACAAACTTTT ?CC?TTAAAC
B. mannii        ATTCTCAACT TTTAT--ACT C??T-----T AAAAATGAAA TGGAGGGCAA CAAAAGAAAG AC?AAGTGTT TCCATTAGAC
B. masoniana     ATTCTCAACT TTTCT--ACT TTTT-----? AAAA?TGAAA TGGAGGGC?A CAAAAAAAA? ACAAAGTTT? -CC-------
B. maynensis     AT?CTCA?CT TTTCT--ACT TTTT-----C AAAAATGA?? TGCAGGGCAA CAAAAGAAAG ACAAAGTTTT TCCATTAGAC
B. meyeri johannis ATTCTCAACT TTTAT--ACT TTT?-----A AAAAA?GAAA TA?AGGGCAA GT?A?GA??? A???AGTTTT TCCGTTAGAC
B. oaxacana      ATTCTCAACT TTTCT--ACT TTTT-----C AAAAATGAAA TGGAGGGCAA CAAAAGAAAG ACAAAGTTTT TCCATTAGAC
B. obliqua       ATTCTCAACT TTTCT--ACT TTTT-----C AAAAATGAAA TGGAGGGCAA CAAAAGAAAG ACAAAGTTTT TCCATTAGAC
B. olbia         ATTCTCAACT T--------- -----AAAAA AAAAATGAAA TGGAGGGCAA CAAAAGAAAG ACAAAGTTTT TCCATTAGAC
B. aff. palmata  ATTCTCAACT TTTCT--ACT T----AAAAA AAAAATGAAA TGGAGGGCA- ---------- ---------- ----------
B. partita       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. peltata       ATTCTCAACT TTTCT--ACT TTTT-----C AAAAATGAAA TGGAGGGCAA CAAAAGAAAG ACAAAGTTTT TCCATTAGAC
B. rajah         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. ravenii       ATTCTCAACT TTTCT--ACT T-----AAAA AAAAATGAAA TGGAGGGCAA CAAAAGAAAG ACCAAGCTTT TCCATTAGAC
B. roxburghii    ATTCTCAACT TTTCT--ACT TTTT-----A AAAAATTAAA TGGAGGGCAA CA?AAGAAAG ACCAAGCTTT TCCATTAGAC
B. rubella       ATTCTCAACT TTTCT--ACT T-----AAAA AAAAATGA?A TGGAGGGCAA CAAAAGAAAG ACCAAGCTTT TCCATTAGAC
B. salaziensis   ATTCTCGACT TTTAT--ACT TTTT-----A AAAAATGAAA TGGAGGCCAC C?AAAGAAAG ACAAAGCTTT TCCATTAGAC
B. sutherlandii  ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. tayabensis    ATTCTCAACT TT-------- ---------- ---------- ---------- ---------- -----GTTTT TCCAGTAAAC
B. ulmifolia     ATTCTCAACT ---------- -----AAAAA AAAAATTAAA TGGAGGGCAA CAAAAGAAAG GCAAAGTTTT ?CCATTAAAC
B. wollnyi       ATTCTCAACT TTTCT--ACT TTTC-----C AAAAATGAAA TGGAGGGCAA CAAAAGAAAG ACAAA?TTTT ----------
Datisca          AT?CTCTATT TTTTTTCACT TTT?-----A CTTAATGAAA TGAAGGGCAA CAAAAGAAA? ACTGGGTCT? ---ATTAT?C
Symbegonia sanguinea ATTCTCAACT TTTCT--ACT TTT-----AA AAAAATGAAA TGGA?GGCAA CAAAAAAAAG ACAAAGTTT? TCCATTAGAC
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APPENDIX K CONTD.

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[                2090       2100       2110       2120       2130       2140       2150       2160]
                    .          .          .          .          .          .          .          .]

B. acerifolia    TCAAAATCAT A-TAAGAATT CATTTGTTAA TTG----ATT GTTTCATCA- ATGGTG---- ---TTGTGCC TGAATTTTAT
B. convolvulacea TCAAAATCAT A-TAAAAATT CGTTTGTTAA TTG----ATT GTTTCATCA- ATGGTG---- ---TTGTGCC TGAATTTTAT
B. dipetala      TGAAAATCAT A-TAAGAACT CGTTTGTTAG TTG----ATT GTTTCATCA- ATGGTGAATG GTGTTGTGCC TGAATTTTTT
B. dregei        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. floccifera    TCAAAATC?T A-TAAGAACT CGTTTGTTAG TTG----ATT GTTTCATCA- ATGGTGAATG GTGTTGTGCC TGAATTTTTT
B. goegoensis    ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. gracilis      TCAAAATCAT A-TAA?AACT CGTTTGTTAG TTG----ATT GTTTCATCA- ATGGTAAATG GTGTTGTGCC TGAATTTTTT
B. cf. grandis   TC?AA?TCAT A-TAAGAACT CGTTTGTTAG TTG----ATT GTTTCATCA- ATGGTGAATG GTGTTGTGCC TGGATTTTTT
B. grandis       TCAAAATCAT A-TAAGAACT CGTTTGTTAG TTG----ATT GTTTCATCA- ATGGTGAATG GTGTTGTGCC ?GGATTTTTT
B. heracleifolia TCAAAATCAT A-TAAGAACT CGTTTGTTAG TTG----ATT GTTTCATCA- ATGGTAAATG GTGTTGTGCC TTAATTTTTT
B. incarnata     TCAAAATCAT A-TAAGAACT CGTTGGTTAG TTG----AT? GTTTCATCA- ATGCTAAATG GTGTTGTGCC TTAATTTTTT
B. malachosticta TCAAAATCAT A-TAAGAACT CGTTTGTTAG TTG----ATT GTTTCATCA- AGGGTGAATG GTGTTGTGCC TTAATTTTTT
B. mannii        TCAA?ATCAT A-TAAGAACT CATTTGTTAC TTG----ATT GTTTCATCA- ATGGTGAATG GTGTTGTGCC TTCATTTTTT
B. masoniana     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. maynensis     TCA?A?TCAT A-TAAGA?CT CGTTTGTTAG TTG----ATT GT?TCATCA- ATGGTAAATG GTGT?GTGCC TGAATTATTC
B. meyeri johannis TCAGAATC-- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. oaxacana      TCAAAATCAT A-TAAGAACT CGTTTGTTAG TTG----ATT GTTTCATCA- ATGGTAAATG GTGTTGTGCC TTAATTTTTT
B. obliqua       TCAAAATCAT A-TAAGAACT CCTTTGTTAG TTG----ATT GTTTCATCA- ATGGTAAATG GTGTTGTGCC TGAATTTTTT
B. olbia         TC?AAATC?T A-TAA?AACT CGTTTGTTAA ---------- ---------- ---------- ---------- ----------
B. aff. palmata  ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. partita       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. peltata       TCAAAATCAT A-TAAGAACT CGTTTGTTAG TTG----ATT GTTTCATCA- ATGGTAAATG GTGTTGTGCC TGAATTTTTT
B. rajah         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. ravenii       TCAAAATCAT A-TAAGAACT CGTTTGTTAG TTG----ATT GTTTCATCA- ATCGTGAATG GTGTTGTGCC TTAATTTTTT
B. roxburghii    TCAAAATCAT A-TAAGAACT CGTTTGTTAG TTG----ATT GTTTCATCA- ATCGTGAATG GTGTTGTGCC TTAATTTTTT
B. rubella       TCAAAATC?T A-TAAGAACT CATTTGTTAG TTG----ATT GTCTCATCA- ATGGTGAATG GTGTTGTGCC TTAATTTTTT
B. salaziensis   TCCAAATC-- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. sutherlandii  ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. tayabensis    TC?AAATCAT A-TAAGAACT CGTTTGTTAG TTG----ATT GTTTCATCA- ATGGTGAATG GTGT?ATGTC TTAATTTTTT
B. ulmifolia     TCAAAATCAT A-TAAAAATT CGTTTGTTAA TTG----ATT CTTTCATCA- ATGGTGAATG GTGTTGTGCC TGAATTTTTT
B. wollnyi       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
Datisca          -CTAC?TGTT AGTAA?A-CT CCCTTGATAC TTCCAA?AAT GTATCCGC?T ATTTT--ATT TACTT?TGC- TTAATGTTTT
Symbegonia sanguinea TCAAAATCAT A-TAAGAACT CGTTTGTTAG TTG----ATT GTTTCATCA- ATGGTGAATG GTGTTGTGCC TTCATTTTTT
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APPENDIX K CONTD.

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[                                2170       2180       2190       2200       2210       2220       2230       2240]
[                    BEG-TRNC3-F-------------------->  .          .          .          .          .          .]

B. acerifolia        TTTT-GACTC TGCACTA?TG ATTTCACTAT TATTAGTGAA CAATAATGAT TAGTGAACAA TAAT------ ----------
B. convolvulacea     TTTT-GACTC TGCACTAGTG ATTTCACTAT TATTAGTGAA CAATAAT--- ---------- ---------- ----------
B. dipetala          TTTT------ ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. dregei            -----GACTC TGCACTATTG ATTTCACTAT TATTAGTGAA CAATAATGAT TAGTGAGCAA TAAT------ ----------
B. floccifera        TTT--GACTC TGCACTAGTG ATTTCA---- ---------- ---------- ---------- ---------- ----------
B. goegoensis        -----GACTC TGCACTATTG ATT?CA?TAT TAT?AGTGA? CAATATTGAT TATTGAACA? TATT------ ----------
B. gracilis          TTTT-GACTC TGCACTAGTG ATTTCACTAT TATTAGTGAA CAATAATGAT TATTGAAAAA TAAT------ ----------
B. cf. grandis       TT---GACTC TGCACTA?TG ATTTCACTAT TATTAGTGA? CAATAATGAT TAGTGAACAA T?TT------ ----------
B. grandis           TTT--GACTC TGCACTAGTG ATTTC----- ---------- ---------- ---------- ---------- ----------
B. heracleifolia     TTT--GACTC TGCACTAGTG ATTTC?CTAT TATTAGTGAA C--------- ---------- ---------- ----------
B. incarnata         TTTTT----- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. malachosticta     TTTT------ ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. mannii            TTTT------ ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. masoniana         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. maynensis         C?C--GACTC TGCACTAGTG ATT?CACTAT TATTAGTCAA CAATAATGAT TAGTGAAAAA GAAT------ ----------
B. meyeri johannis   ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. oaxacana          TTT--CACTC TGCACTAGTG ATTTCACTAT TATTAGTGAA CAATAATGAT TAGTGAACAA TAATGATTA? TGAAAAATAA
B. obliqua           TTTT-GACTC TGCACTAGTG ATTTCACTAT TATTAGTGAA CAATAATGAT TTGTGAAAAA TAAT------ ----------
B. olbia             ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. aff. palmata      ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. partita           -----GACTC TGCACTA?TG ATTTCACTAT TATTAGTGAA CAATAATGAT TAGTGAGCAA TAAT------ ----------
B. peltata           TTTT-CACTC TGCAGTAGTG ATTTCACTAT TATTAGTGAA CAATAATGAT TAGTGAACAA TAATGATTAG TGAAAAATAA
B. rajah             -----GACTC TGCACTAGTG ATTTCACTAT TATTAGTGAA CAATAATGAT TAGTGAACAA TAAT------ ----------
B. ravenii           TTT--GACTC TGCACTAATA ATTTCACTAT TATTAGTGAA CAATAATGAT TAGTGAAC?G TAAT------ ----------
B. roxburghii        TTT------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. rubella           TTT--GACTC TGCACTA?TA ATTTCCCTAT TATTAGGGAA C?AT?ATGAT T?GTGAAC?? TAAT------ ----------
B. salaziensis       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. sutherlandii      -----GACTC TGCACTATTG ATTTCACTAT TATTA?TGA? CAATATTGAT TATTGAACAA TAAT------ ----------
B. tayabensis        TTTT------ ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. ulmifolia         TTTT-GACTC TGCACTATTG ATTTCACTAT TATTAGTGAA CAATAATGAT TA?TGAACAA TAAT------ ----------
B. wollnyi           ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
Datisca              TT-------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
Symbegonia sanguinea TTTT-CACTC TGCAC----- ---------- ---------- ---------- ---------- ---------- ----------
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APPENDIX K CONTD.

	2250	2260	2270	2280	2290	2300	2310	2320
B. acerifolia	-GGAATAATT	CTTTTATATT	CATA?AGAT?	GGGGACATAA	TTCACATGGA	TATAGTAAGT	CTCGCTTGGG	CTGCTTTAAT
B. convolvulacea	-GGAATAATT	CTTTTATATT	CATAGAGATA	GGGGACATAA	TTCACATGGA	TATAGTAAGT	CTCGCTTGGG	CTGCTTTAAT
B. dipetala	----------	----------	----------	----------	----------	----------	----------	----------
B. dregei	-GGAATAATT	CTTTTATATT	CATAAAAATA	GGGGACATAA	TTCACATGGA	TATAGTAAGT	CTCGCTTGGG	CTGCTTTAAT
B. floccifera	----------	----------	----------	----------	----------	----------	----------	----------
B. goegoensis	----------	----------	----------	----------	----------	----------	----------	----------
B. gracilis	-GGAATAATT	CTTTTATATT	C?TAAAGATA	GGGGACATAA	TTCACATGGA	TATAGTAAGT	CTCGCTTGGG	CTGCTTTAAT
B. cf. grandis	----------	----------	----------	----------	----------	----------	----------	----------
B. grandis	----------	----------	----------	----------	----------	----------	----------	----------
B. heracleifolia	----------	----------	----------	----------	----------	----------	----------	----------
B. incarnata	----------	----------	----------	----------	----------	----------	----------	----------
B. malachosticta	----------	----------	----------	----------	----------	----------	----------	----------
B. mannii	----------	----------	----------	----------	----------	----------	----------	----------
B. masoniana	----------	----------	----------	----------	----------	----------	----------	----------
B. maynensis	-GGAATAAT?	CTTTTATATT	CATAGAGATA	GGGGACATAA	TTCACATGGA	T?TA?TAAGT	CTCGCTTGGG	CTGCTTTAAT
B. meyeri johannis	----------	----------	----------	----------	----------	----------	----------	----------
B. oaxacana	TGGAATAATT	CTTTTATATT	CATA?AGATA	GGGGACATAA	TTCACATGGA	TATAGTAAGT	CTCGCTTGGG	CTGCTTTAAT
B. obliqua	-GGAATAATT	CTTTTATAT?	CATA?A?ATA	GGGGACATAA	TTCACATGGA	TATTGTAAGT	CTCGCTTGGG	CTGCTTTAAT
B. olbia	----------	----------	----------	----------	----------	----------	----------	----------
B. aff. palmata	----------	----------	----------	----------	----------	----------	----------	----------
B. partita	-GGAATAAT?	CTTTTATAT?	CATAAAAATA	GGGGACATAA	TTCACATGGA	TATA?TAA?T	CTCGCTTGGG	CTGCTTTAAT
B. peltata	TGGAATAATT	CTTTTATAT?	CATAGAGATA	GGGGACATAA	TTCACATGGA	TATAGTAAGT	CTCGCTTGGG	CTGCTTTAAT
B. rajah	-GGAATAATT	CTTTTATATC	CATAGAGATA	GGGGACATGA	TTCACATGGA	TATAGTAAGT	CTCGCTTGGG	CTGCTTTAAT
B. ravenii	-GGAATA?TT	ATTTTATATT	CAT?CACATA	GGGGACATAA	TTTACATGGA	TATGGTAAGT	CTCGCTTGGG	CTGCTTTAAT
B. roxburghii	----------	----------	----------	----------	----------	----------	----------	----------
B. rubella	-GGAATA---	----------	----------	----------	----------	----------	----------	----------
B. salaziensis	----------	----------	----------	----------	----------	----------	----------	----------
B. sutherlandii	-GGAATAATC	CTTTTAT?TC	C?TAAAAAT?	GGGGACATA?	TCC?C?TGGA	T?TATTAAGT	CTCGCT?GGC	CTCCTTTAA?
B. tayabensis	----------	----------	----------	----------	----------	----------	----------	----------
B. ulmifolia	-GGAATAATT	ATTTTATATT	CATA------	----------	----------	----------	----------	----------
B. wollnyi	----------	----------	----------	----------	----------	----------	----------	----------
Datisca	----------	----------	----------	----------	----------	----------	----------	----------
Symbegonia sanguinea	----------	----------	----------	----------	----------	----------	----------	----------

APPENDIX K CONTD.

```
[                2330       2340       2350       2360       2370       2380       2390       2400]
!                   .          .          .          .          .          .          .          .!

B. acerifolia    GGTAGTCTTT ACATTTTCCC TTTCACTCGT AGTATGGGGA AGAAGTGGAC TCT------- ---------- ----------
B. convolvulacea GGTAGTCTTT ACATTTTCCC TTTCACTCGT AGTATGGGGA AGAAGTGGAC TCT------- ---------- ----------
B. dipetala      ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. dregei        GGTAGTCTTT ACATTTTCCC TTTCACTCGT A?TATGGGGA AGAAGTGGAC TCTAAAAGTA CTACTAATTG AGGAATCAAC
B. floccifera    ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. goegoensis    ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. gracilis      GGTAGTCTTT ACATTTTCCC TTTCACTCGT AGTATGGGG- ---------- ---------- ---------- ----------
B. cf. grandis   ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. grandis       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. heracleifolia ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. incarnata     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. malachosticta ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. mannii        ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. masoniana     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. maynensis     GGTAGTCTTT ACATTTTCCC TTTCACTCGT AGTATGGGGA AGAA?TGGAC TC??AAAGTA CTACTAATTG AGGAATCAAC
B. meyeri johannis ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. oaxacana      GGTAGTCTTT ACA------- ---------- ---------- ---------- ---------- ---------- ----------
B. obliqua       GGTA------ ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. olbia         ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. aff. palmata  ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. partita       GGTA?TCTTT ACATTT?CCC TTTCACTCGT ATTATGGGGA A?AA?TGGAC TCTAAAATTA CTACTAATTG AGGAATCAAC
B. peltata       GGTAGTCTT- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. rajah         GGTAGTCTTT ACATTTTCCC TTTCACTCGT A?TATCGGGA AGAAGTGGAC TCTAAAAGTA CTACTAATTG AGGAATCAAC
B. ravenii       GGTAGTC?TT ACATTT?CCC TTTCCCTCGT AGTAT----- ---------- ---------- ---------- ----------
B. roxburghii    ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. rubella       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. salaziensis   ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. sutherlandii  CGTATTCTTT AC-TTTTCCC CTTCAC?CGT ATTATGGGGA AAAATTG?AC ?C?AAAATTT CT?CTATTTG AGGA??CACC
B. tayabensis    ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. ulmifolia     ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
B. wollnyi       ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
Datisca          ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
Symbegonia sanguinea ---------- ---------- ---------- ---------- ---------- ---------- ---------- ----------
```

APPENDIX K CONTD.

```
[                          2410        2420        2430        2440        2450]
[                            .           .           .           .           .]

B. acerifolia              ---------- ---------- ---------- ---------- ----------
B. convolvulacea           ---------- ---------- ---------- ---------- ----------
B. dipetala                ---------- ---------- ---------- ---------- ----------
B. dregei                  CTCAAACTGT ATCAATTGTT TTATA?ATTG TTCTGCCGAG CCTTTTTTTT
B. floccifera              ---------- ---------- ---------- ---------- ----------
B. goegoensis              ---------- ---------- ---------- ---------- ----------
B. gracilis                ---------- ---------- ---------- ---------- ----------
B. cf. grandis             ---------- ---------- ---------- ---------- ----------
B. grandis                 ---------- ---------- ---------- ---------- ----------
B. neracleifolia           ---------- ---------- ---------- ---------- ----------
B. incarnata               ---------- ---------- ---------- ---------- ----------
B. malachosticta           ---------- ---------- ---------- ---------- ----------
B. mannii                  ---------- ---------- ---------- ---------- ----------
B. masoniana               ---------- ---------- ---------- ---------- ----------
B. maynensis               CTCAAACTGT ATCAATAGTT TTATA?ATTG TTCTGCCGAG CCTTTTT---
B. meyeri-johannis         ---------- ---------- ---------- ---------- ----------
B. oaxacana                ---------- ---------- ---------- ---------- ----------
B. obliqua                 ---------- ---------- ---------- ---------- ----------
B. olbia                   ---------- ---------- ---------- ---------- ----------
B. aff. palmata            ---------- ---------- ---------- ---------- ----------
B. partita                 CTCAAACTGT ATCAATTGTT TTATA?ATTG TYCTGCCGA? CCTTTTTTTT
B. peltata                 ---------- ---------- ---------- ---------- ----------
B. rajah                   CTC?AAATGT ATCAATTGGT TTATA?ATTG TTCTGCCGAG CCT?TTTTTT
B. ravenii                 ---------- ---------- ---------- ---------- ----------
B. roxburghii              ---------- ---------- ---------- ---------- ----------
B. rubella                 ---------- ---------- ---------- ---------- ----------
B. salaziensis             ---------- ---------- ---------- ---------- ----------
B. sutherlandii            C?CAAACT?T T?CA?TT?TT TTATAAATT? TTCTGCC?A? CC?TTTTTTT
B. tayabensis              ---------- ---------- ---------- ---------- ----------
B. ulmifolia               ---------- ---------- ---------- ---------- ----------
B. wollnyi                 ---------- ---------- ---------- ---------- ----------
Datisca                    ---------- ---------- ---------- ---------- ----------
Symbegonia sanguinea       ---------- ---------- ---------- ---------- ----------
```

APPENDIX L RFLP DATA FOR TRNC - TRND (TEBBITT, 1997)

B. chlorosticta	0000110101 101011
B. dregei	1111101001 011011
B. floccifera	1000110111 100011
B. goegoensis	0111111111 100011
B. grandis	1000111111 101011
B. hatacoa	1000010110 100011
B. incarnata	1111111101 011111
B. mannii	1100110101 101101
B. masoniana	0000110111 111011
B. meyeri-johannis	0110111101 111011
B. roxburghii	1000010110 101011
B. salaziensis	1000110101 101011
B. sutherlandii	1111101001 011010
B. tayabensis	0001111101 101011

APPENDIX M: INDEL DATA SET

	61-225	85	104-108	113-121	124	128-137	138-143	161-172	165-169	178-195	186-192	200	304-306	317-463	343-344	348	349-357	358-362	381	408-410	411	432	436-450	475	492-496	497-503	525-540	559-564	616-617	627-630	647	674	676	679-686	699	704-705	706	712	713
B. acerifolia	1	0	0	0	1	1	0	1	0	1	0	1	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	?	?	?	?	?	?	?	?	?
B. acutifolia	1	0	1	0	1	1	0	1	0	1	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	0	1	1	1
B. cf. grandis	1	0	1	0	1	0	0	1	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	0	1
B. aff. palmata	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1
B. convolvulacea	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1	1	1
B. dipetala	1	0	1	0	1	1	0	1	1	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1
B. dregei	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1
B. floccifera	1	0	1	0	1	1	0	1	0	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1
B. goegoensis	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1
B. gracilis	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	0	1	1	1
B. grandis	1	0	1	0	1	0	0	1	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	1
B. heracleifolia	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1
B. incarnata	1	0	1	0	1	1	1	1	0	1	0	1	0	0	?	?	?	?	?	?	?	?	?	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1
B. malachosticta	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1
B. mannii	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	1	1	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1
B. masoniana	0	?	?	?	?	?	?	?	?	?	?	?	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1
B. maynensis	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1
B. meyeri-johannis	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	1	1	0	1	0	0	0	0	1	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1
B. oaxacana	1	0	0	0	0	1	0	1	0	1	0	1	0	1	1	0	0	0	1	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. olbia	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1
B. partita	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1
B. peltata	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1
B. rajah	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1
B. ravenii	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1
B. roxburghii	1	0	1	0	1	1	0	0	?	1	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	1
B. rubella	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1	0	1	1	1
B. salaziensis	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	0	1	1
B. sutherlandii	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1
B. tayabensis	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1
B. ulmifolia	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1
B. wollnyi	?	?	?	?	?	?	?	?	?	?	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1
Datisca	1	1	1	1	1	1	0	1	0	0	0	0	0	1	1	1	1	0	1	1	1	1	0	0	0	1	0	1	0	0	1	1	1	0	1	1	1	1	0
Symbegonia sanguinea	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1

APPENDIX M: INDEL DATA SET

	705-707	718-722	723-738	739	740-944	902-944	945-973	978-983	1246	1252	1263-1269	1276-1281	1282-1290	1291-1292	1329-1333	1343-1848	1353-1357	1364-1373	1411-1423	1446-1650	1481-1485	1486-1508	1509-1553	1557-1735	1590-1591	1602-1609	1813	1615-1622	1635-1773	1657-1661	1671	1672-1687	1712-1714	1719-1742	1722-1726	1735-1792	1736-1740	1751-1755	1756
B. acerifolia	?	?	?	?	?	?	?	?	0	0	1	1	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. acutifolia	1	1	0	1	0	1	1	1	0	0	1	1	0	1	1	1	1	1	0	1	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. cf. grandis	1	1	0	1	0	?	?	?	0	0	1	1	0	1	1	1	1	1	0	1	0	0	0	1	0	1	1	0	1	0	1	0	1	1	0	1	0	1	1
B. aff. palmata	1	1	0	1	0	1	1	1	0	0	1	1	0	1	1	1	1	1	0	1	0	0	0	1	0	1	1	0	1	0	1	0	1	1	0	0	?	?	?
B. convolvulacea	1	1	0	1	0	?	1	1	0	0	1	1	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. dipetala	1	1	0	1	0	?	?	?	0	0	1	1	0	1	1	1	1	1	0	1	0	0	0	1	0	1	1	0	1	0	1	0	1	1	0	1	0	1	1
B. dregei	1	1	0	1	0	1	1	1	0	0	1	1	0	1	1	1	1	1	0	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	1	0	0	0
B. floccifera	1	1	0	1	0	0	0	1	0	0	1	1	0	1	1	1	1	1	0	1	1	0	0	1	0	1	1	0	1	0	1	0	1	1	0	1	0	1	1
B. goegoensis	1	1	0	1	0	1	1	0	0	0	1	1	0	1	1	1	1	1	1	1	0	0	0	1	0	1	1	0	1	0	1	0	1	1	0	1	0	1	1
B. gracilis	1	1	0	1	1	1	1	1	0	0	1	1	0	1	1	1	1	1	0	1	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. grandis	1	1	0	1	0	1	1	1	0	0	1	1	0	1	1	1	1	1	0	1	0	1	0	1	0	1	1	0	1	0	1	0	1	1	0	1	0	1	1
B. heracleifolia	1	?	?	?	?	?	?	?	?	?	?	1	0	1	1	1	1	1	0	1	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. incarnata	1	0	0	0	0	?	1	1	0	0	1	1	0	1	1	1	1	1	0	1	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. malachosticta	1	1	0	1	0	?	?	?	0	0	1	1	0	1	1	1	1	1	1	1	0	0	0	1	0	1	1	0	1	0	1	1	1	1	0	1	0	1	1
B. mannii	1	1	0	1	0	1	1	1	0	0	0	1	0	1	1	1	1	1	0	1	0	0	0	1	0	1	1	0	1	0	1	0	1	1	0	1	0	1	1
B. masoniana	1	1	0	1	0	?	?	?	0	0	1	1	0	1	1	1	1	1	1	1	0	0	0	1	0	1	1	0	1	0	1	0	1	1	0	1	0	1	1
B. maynensis	1	1	0	1	0	1	1	1	0	0	1	1	0	1	1	1	1	1	0	1	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. meyeri-johannis	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	0	1	1
B. oaxacana	?	?	?	?	?	?	?	?	0	0	1	1	0	1	1	1	1	1	0	1	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. olbia	1	1	0	1	0	1	1	1	0	0	1	1	0	1	1	1	1	1	0	1	0	0	0	1	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?
B. partita	1	1	0	1	0	1	1	1	0	0	1	1	0	1	1	1	1	1	0	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	1	0	0	1
B. peltata	1	0	0	0	0	?	1	1	0	0	1	1	0	1	1	1	1	0	0	1	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. rajah	1	1	0	1	0	1	1	1	?	?	?	1	0	1	1	1	1	1	1	1	0	0	0	1	0	1	1	0	1	0	1	0	1	1	0	1	0	1	1
B. ravenii	1	1	0	1	0	1	1	1	0	0	1	1	0	1	1	1	1	1	0	1	0	0	0	1	0	1	1	0	1	0	1	0	1	1	0	1	0	1	1
B. roxburghii	1	1	0	1	0	1	1	1	0	0	1	1	0	1	1	1	1	1	0	1	0	0	0	1	0	1	1	0	1	0	1	0	1	1	0	0	?	?	?
B. rubella	1	1	0	1	0	1	1	1	0	0	1	1	0	1	1	1	1	1	0	1	0	0	0	1	0	1	1	0	1	0	1	0	1	1	0	1	1	1	1
B. salaziensis	1	1	0	1	0	?	?	?	?	?	?	1	0	1	1	1	1	1	0	0	?	?	?	?	?	?	?	?	1	0	1	0	1	1	1	1	0	1	1
B. sutherlandii	1	1	0	1	0	?	?	?	0	0	1	1	0	1	1	1	1	1	0	1	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. tayabensis	1	1	0	1	0	?	?	?	0	0	1	1	0	1	1	1	1	1	1	1	0	0	0	1	0	0	1	0	1	0	0	0	1	1	0	1	0	1	1
B. ulmifolia	1	1	0	1	0	1	1	1	0	0	1	1	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. wollnyi	1	1	0	1	0	?	?	?	0	0	1	1	0	1	1	1	1	1	0	1	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Datisca	1	1	1	1	1	?	?	?	1	1	1	0	?	0	0	1	0	1	0	1	0	0	0	1	1	1	1	1	1	1	1	0	0	0	?	?	?	1	1
Symbegonia sanguinea	1	1	0	1	0	1	1	1	0	0	1	1	0	1	1	1	1	1	1	1	0	0	0	1	0	1	1	0	1	0	1	0	1	1	0	1	0	1	1

APPENDIX M: INDEL DATA SET

	1757-1761	1762-1767	1768-1772	1773-1778	1793-2165	1809-1812	1825-1827	1828-1838	1843-1845	1860-1863	1863-2065	1882-1883	1925-1929	1832	1871	1978	1981-1988	2012-2021	2016-2017	2022-2065	2071	2072-2073	2081	2092	2098	2114-2117	2130	2136	2137	2138-2143	2150	2208-2224	2225-2242
B. acerifolia	?	?	?	?	?	?	?	?	?	1	1	1	0	0	0	0	0	0	?	1	1	1	1	0	1	0	0	1	0	0	1	0	0
B. acutifolia	?	?	?	?	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	1	1	1	1	?	?
B. cf. grandis	1	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	1	1	1	1	1	0
B. aff. palmata	?	?	?	?	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. convolvulacea	?	?	?	?	?	?	?	?	?	1	1	1	0	0	0	0	0	0	?	1	1	1	1	0	1	0	0	1	0	0	1	0	0
B. dipetala	1	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	1	1	1	1	?	?
B. dregei	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?
B. floccifera	1	1	1	1	1	1	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	1	1	1	1	?	?
B. goegoensis	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?
B. gracilis	?	?	?	?	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	1	1	1	1	1	0
B. grandis	1	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	1	1	1	1	?	?
B. heracleifolia	?	?	?	?	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	1	1	1	1	?	?
B. incarnata	?	?	?	?	1	0	0	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. malachosticta	1	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	1	1	1	1	?	?
B. mannii	1	0	0	0	1	0	1	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	1	1	1	1	?	?
B. masoniana	1	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?
B. maynensis	?	?	?	?	1	0	0	0	0	1	1	0	1	0	0	0	0	1	0	1	1	1	1	0	1	0	0	1	1	1	1	1	0
B. meyeri-johannis	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	?	?	?	?	?	?	?	?	?	?
B. oaxacana	?	?	?	?	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	1	1	1	1	1	1
B. olbia	?	?	?	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0	?	1	1	1	1	0	1	?	?	?	?	?	?	?	?
B. partita	1	1	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?
B. peltata	?	?	?	?	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	1	1	1	1	1	1
B. rajah	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?
B. ravenii	1	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	1	1	1	1	1	0
B. roxburghii	?	?	?	?	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	1	1	1	1	?	?
B. rubella	1	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	1	1	1	1	1	0
B. salaziensis	1	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	?	?	?	?	?	?	?	?	?	?
B. sutherlandii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?
B. tayabensis	1	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	?	0	1	1	1	0	1	0	0	1	1	1	1	?	?
B. ulmifolia	?	?	?	?	?	?	?	?	?	1	1	1	0	0	0	0	0	0	?	1	1	1	1	0	1	0	0	1	1	1	1	1	0
B. wollnyi	?	?	?	?	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?
Datisca	1	0	0	0	1	0	0	1	1	0	1	1	0	1	1	1	1	1	1	1	0	0	0	1	0	1	1	0	0	1	0	?	?
Symbegonia sanguinea	1	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	1	1	1	1	?	?